University of Alberta

The importance of fire-skips as biotic refugia and the influence of forest heterogeneity on epigaeic beetles in pyrogenic stands of the northern Rocky Mountains

by

Kamal Jit Kaur Gandhi ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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DEDICATION

To my parents,
Balwinder and Fateh,
for their love and patience

ABSTRACT

Litter-dwelling beetles (Coleoptera: Carabidae and Staphylinidae) were studied in residual patches of unburned forest (fire-skips) left by two natural wildfires in high-elevation coniferous forests to explore the importance of fire-skips as biotic refugia. Fire-skips were wet, late-successional forest patches that provided habitats for large number of beetle species. The largest fire-skips were the oldest stands on the pyrogenic landscape. No relationships were found between the size of fire-skips and total beetle richness or activity. However, higher numbers of some beetle species were collected in larger skips. Both fire-skips and the unburned mature forest were important sources for beetle recolonization of the regenerating forest.

Forest composition (overstory and understory diversity) and forest structure reflected in attributes of vegetation were correlated with beetle catches and diversity. Thus, epigaeic beetles required a range of key-habitat attributes in forest ecosystems.

Forest harvest practices attempting to mimic landscape patterns of natural disturbances, should include leaving retention patches equivalent to fire-skips. Range of habitat and structural variability present within forest patches may also be important for maintaining fauna in landscapes affected regularly by wildfire.

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Chapter 1 . Thesis Introduction

1.1 Research Rationale

Natural disturbance is defined as 'a relatively discrete event in time that disrupts ecosystem, community or population structure, and changes resources, substrate availability, or the physical environment' (Pickett and White 1985). It is a major driving force influencing landscape structure and ecosystem processes in northern forests. Large disturbances such as wildfires and insect outbreaks create shifting habitat mosaics of differently aged trees and forest types on the landscape (Hunter 1993, Haila *et al.* 1994). Clearly, biotic assemblages that characterize these forests must be adapted to natural disturbance events that re-start local succession periodically (Holliday 1991, 1992, Muona and Rutanen 1994).

In the montane and sub-alpine forests of the Canadian Rocky Mountains, natural disturbances are being augmented and potentially replaced by anthropogenic disturbances, primarily forest harvesting as the predominant stand initiating events. Never-cut high-elevation forests that cover about 150,000 square kilometers or 22% of Alberta's land area (Urquhart 1998) are now under major economic pressure. In addition to oil, gas exploration and ranching, Annual Allowable Cuts (AAC) of more than 3 million cubic meters of standing fibre are being harvested yearly as part of the Forest Management Agreements (FMAs) (Alberta Environment 1998). Such large-scale forest

development activities have raised significant concerns about the resilience and sustainability of these ecosystems.

Harvesting practices such as clear-cutting have often been rationalized as equivalent to wildfire in terms of habitat disturbance and, by inference, the resulting impacts on forest biodiversity. However, harvesting establishes more homogenous stands, and leaves less woody debris and living foliage than wildfires (Zackrisson 1977, Haila *et al.* 1994). Such spatial changes may have different consequences for natural biota that require specific forest attributes such as burned and decayed coarse-woody debris, specialized micro-habitats found in ecosystems created by natural disturbances (Speight 1989, Wilson 1992, Haila and Kouki 1994).

Forest managers are adopting the 'natural disturbance paradigm' (NDP) in an attempt to retain the temporal and spatial complexity created by wildfire on harvested landscapes, while extracting forest fibre (Thompson and Welsh 1993). Emulating a natural disturbance is widely thought to be a reasonable approach to ecologically sound management in high-elevation forests (Weyerhaeuser Canada 1997). This paradigm suggests leaving a range of residual forest, including dead material such as snags, logs, live trees, and undergrowth on harvested blocks to act as faunal 'store-houses' equivalent to residual forest fragments or 'fire-skips', left naturally after a wildfire. Such forest patches may act as reserves for biological diversity, and permit rapid recolonization of the surrounding forest as it regenerates.

Although the natural disturbance model is being widely employed in boreal and montane forests, few studies have been done of the biota of fire-skips of natural pyrogenic landscapes (Ohlson *et al.* 1997, Hörnberg *et al.* 1998). It is presently unknown if fire-skips are important refugia for forest dependent species, especially woodland fauna with lower dispersal rates and that would be adversely affected by harvesting practices on a regional scale (Hanski and Hammond 1995). Furthermore, landscape-position, variation in stand-type, and size of retention blocks may also be serious considerations in harvest plans. Therefore, to provide an understanding of the ecological processes occurring on pyrogenic landscapes, I studied beetle assemblages (Coleoptera: Carabidae and Staphylinidae, excluding Subfamily Aleocharinae) of fire-skips in two coniferous stands of different ages (15 and 36 year old burns) on the eastern, sub-alpine slopes of the Rocky Mountains (Figures 1.1 - 1.3).

Habitat heterogeneity is an inherent part of pyrogenic stands (Hunter 1993, Haila *et al.* 1994, Bunnell 1995), and the associated variation in forest attributes may be important determining factors for species distributions. To better emulate natural disturbances in harvest regimes, habitat heterogeneity and its influence on biota needs to be considered. Therefore, a separate study was undertaken at the two burns to understand whether habitat attributes, such as forest structure and composition, influence patterns of beetle activity and diversity.

1.2 Study Taxa

Conservation and forest management programs in the past have primarily targeted large and conspicuous animals such as birds and mammals. However, the ecological importance of invertebrates that numerically and functionally dominate the terrestrial ecosystems is increasingly being recognized (Wilson 1992, Kremen *et al.* 1993). Danks and Foottit (1989) estimated that *c.* 22,000 species of insects occur in Canada's boreal forests, but the numbers in sub-alpine and montane forests are presently unknown. Epigaeic or litter-dwelling insects such as ground (Carabidae) and rove (Staphylinidae) beetles play well-documented roles in nutrient cycling, breakdown of coarse-woody debris and overall maintenance of forest health (Stork 1990, Buse and Good 1993, Spence *et al.* 1996, 1997). As important elements in forest ecosystems, these assemblages of soil-inhabiting beetles are sensitive to changes to environment quality and habitat structure. Thus, they are potential 'indicator taxa' (Pearson 1994, McGeoch 1998) and are relevant to forest management practices.

1.3 Thesis Objectives

The general objectives of this thesis are:

1. To determine whether fire-skips are habitat reserves for beetle species;
2. To assess the recolonization patterns of beetle species at the edges between the burn and the surrounding unburned mature forest, and between the fire-skips and the burned forest;

3. To explore whether species richness or activity-abundance patterns of beetles are related to fire-skip size;
4. To assess the stand age of fire-skips and the surrounding unburned forest;
5. To determine whether beetle diversity and catches are correlated with forest composition and/or structure.

Chapter two focuses on the role of fire-skips as biotic refugia for beetle species, beetle recolonization patterns of the burned forest, and relationships between beetle species richness and skip-area at the two study sites of different age. I also deal with the ages of trees in the surrounding unburned forest and fire-skips, and the relationship between tree age and fire-skip sizes.

Chapter three focuses on the importance of habitat heterogeneity in terms of forest structure and composition for beetle assemblages. Forest attributes, the independent variables, measured in the fire-skips, unburned and the burned forest were coarse-woody debris, plant and tree species, moss, grass, lichen, and shrub cover, while beetle diversity, dominance measures and activity were the dependent variables.

In chapter four, I summarize and discuss the most important results of this two-year study, and place them in the context of forest management practices in pyrogenic, high-elevation, coniferous forests.

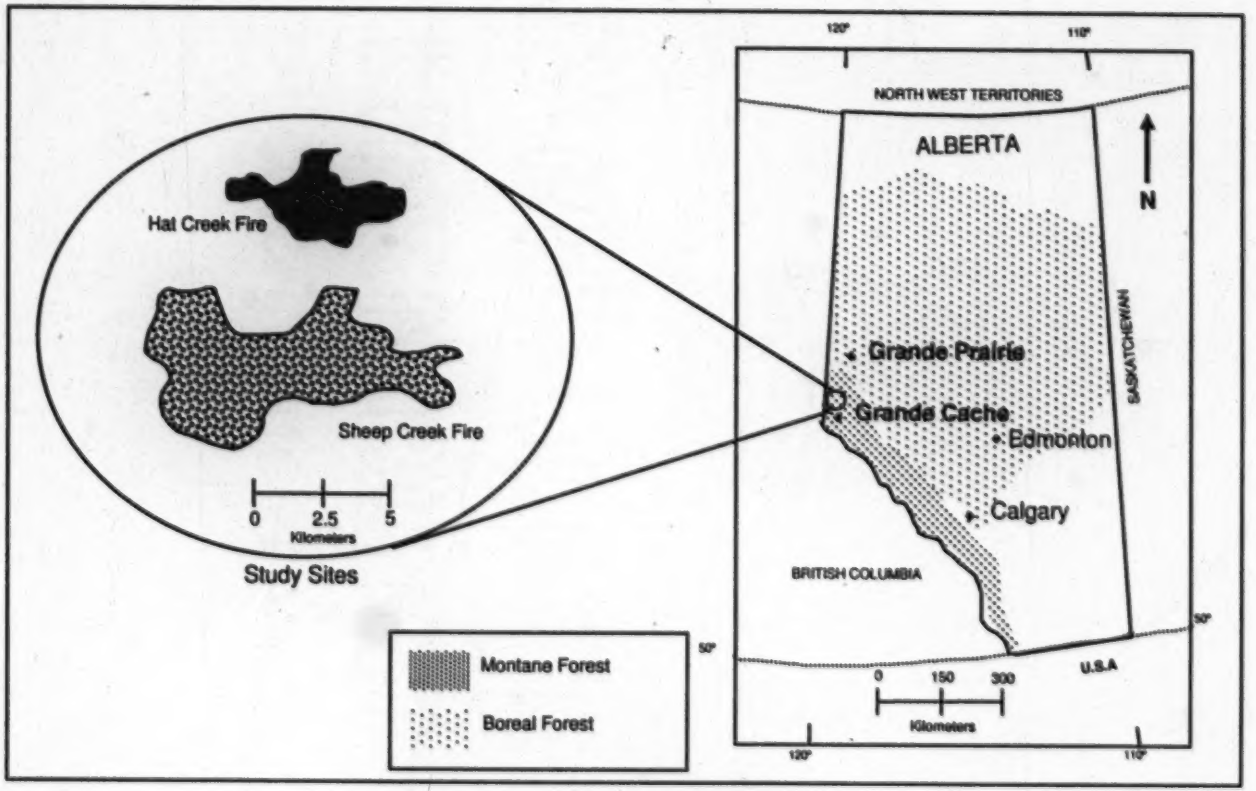

Figure 1.1. Location of study sites in Alberta.

Figure 1.2. Air-photographs showing fire-skips in the Hat Creek burn. Numbers refer to individual fire-skip examined. For areas of each fire-skip, also see Table 2.

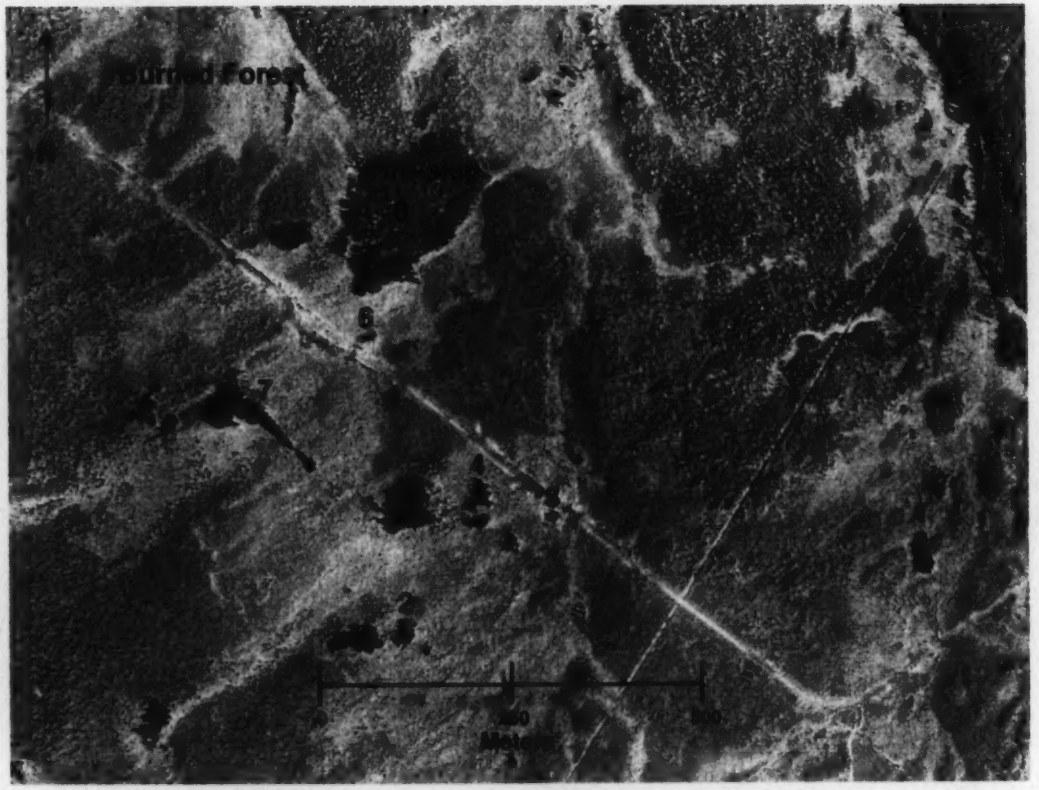

Figure 1.3. Air-photographs showing fire-skips in the Sheep Creek burn. Numbers refer to individual fire-skip examined. For areas of each fire-skip, also see Table 2.

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Chapter 2. Fire-skips as Habitat Reserves for Epigaeic Beetles

2.1 Synopsis

To explore the importance of fire-skips as biotic refugia, litter-dwelling beetles (Coleoptera: Carabidae and Staphylinidae) were studied in residual patches of unburned forest (fire-skips) left by two natural wildfires in high-elevation coniferous forests. Fire-skips were found to be wet, late-successional patches of fir and spruce forests and provided habitats for viable populations of larger number of forest-dwelling beetle species such as *Calathus advena, Calathus ingratus, Elaphrus lapponicus, Mycetoporus americanus, Nebria crassicornis, Olorphrum rotundicolle, Pterostichus empetricola, Pterostichus haematopus, Quedius densiventris and Tachinus frigidus*. The largest fire-skips contained the oldest living trees and were thus, the oldest stands on the pyrogenic landscape. Although there was no relationship between the size of fire-skips and beetle diversity or total activity, more *N. crassicornis* and *Q. densiventris* were collected per trap in larger skips suggesting their dependence on late-seral stage attributes present within the largest skips. Patchily distributed fire-skips within the burned forest and the surrounding mature forest were important sources for recolonization of the regenerating forest. Conservation of equivalent sites during forest harvest activities would provide analogues for fire-skips, contributing to landscape

continuity and preservation of faunal elements common in wildfire-origin landscapes.

2.2 Introduction

Large-scale forest harvesting is augmenting natural disturbance as a stand initiator in western Canadian forests (Pratt and Urquhart 1994, Urquhart 1998). Resulting shifts in inherent forest dynamics, such as truncation of stand age and associated loss of forest cover, may result in significant biotic improvishment of forested ecosystems (Franklin 1989, Wilson 1992). If wildfire is suppressed significantly to balance the loss of forest habitat, fire-adapted and early successional species dependent on special microhabitats and coarse-woody debris in fire-origin landscapes may be adversely affected (Holliday 1991, 1992).

Natural disturbances, including small gap-dynamics such as windfalls, and larger disturbances like insect outbreaks and wildfires, create shifting habitat mosaics across the landscape (Hunter 1993, Haila *et al.* 1994, Bunnell 1995). In an attempt to preserve structural complexity on landscapes, forest managers are adopting the 'natural disturbance paradigm' that hinges on retaining small patches of uncut forest (including undergrowth, and live and dead trees) within harvested areas. These unharvested residuals are considered comparable to 'fire-skips' or unburned islands of forest left naturally by wildfires. It is assumed that local biotas are adapted to landscape patterns produced by periodic wildfire, and hypothesized that leaving forest

patch analogues of fire-skips will promote short-term conservation and improve the regeneration of harvested ecosystems. There are many studies of the effect of clear-cutting and fragmented landscapes on biotic elements (Harris 1984, Quinn and Harrison 1987, Bierregard *et al.* 1992), but few on the effects of wildfire (Holliday 1991, 1992, McCullough *et al.* 1998), and even fewer on naturally fragmented biotopes like fire-skips.

Development of effective prescriptions to emulate fire-skips depends on our understanding of ecological processes and biotic functions in fire-skips. For example, leaving patches in harvested blocks would be futile if potentially threatened species dependent on forests do not use them, or if they remain stranded within these islands with little inter-patch movement and recolonization of the regenerating forest. Even if fire-skips prove to be ecologically important habitats within a pyrogenic landscape, forest managers would further need to know the ideal dimensions, number and landscape locations of potential forest residuals.

I studied the epigaeic arthropod assemblages of fire-skips in two pyrogenic stands of high-elevation coniferous forests in the Canadian Rockies. Specifically, the research objectives of this two year study were: (1) to assess the stand age of fire-skips relative to that of surrounding unburned forest; (2) to determine whether fire-skips are important habitat reserves for epigaeic beetle assemblages; (3) to assess the distribution patterns of beetle species in the surrounding unburned forest and fire-skip edges in relation to

recolonization of the burned forest and; (4) to explore whether species richness and activity-abundance patterns are related to skip-size.

2.3 Methods

2.3.1 Study Organisms

Disturbance events including wildfire and harvesting alter the physical and chemical properties of the forest soil and litter (Kubin and Kemppainen 1991, Cortina and Vellaejo 1994). Because of these changes on the forest floor, epigaeic or surface-dwelling fauna may have the potential to act as 'indicator taxa' for studies of such disturbances (McGeoch 1998). Among epigaeic groups, carabids (ground beetles) and staphylinids (rove beetles, excluding the Subfamily Aleocharinae) are ideal organisms for this study because they are relatively stable taxonomically, speciose, easily caught in pitfall traps and are known to be sensitive to environmental change (Arnett 1968, Nield 1990, Buse and Good 1993, Niemelä *et al.* 1993, Spence *et al.* 1996). Together they represent a range of diverse feeding niches including carnivory, fungivory and herbivory (Spence *et al.* 1997), and of flight or dispersal capability. This enables the researcher to understand and make inferences about the effects of disturbances on a broader level.

2.3.2 Study Sites

Epigaeic beetle assemblages were sampled at two study sites in the sub-alpine zone (1,525 - 1,710 meters elevation) on the east slopes of the Rocky Mountains in western Alberta, Canada: (1) the Hat Creek Fire (54° 1391' N, 119° 4215' W), which burned in 1982, was sampled in 1997 (15 years post-burn) and, (2) the Sheep Creek Fire (54° 055' N, 119° 10' W), which burned in 1962, was sampled in 1998 (36 years post-burn). Both burns are located north of Grande Cache and southwest of Grande Prairie in the Weyerhaeuser Forest Management Area (Figure 1.1). Comparisons between recovering forests of different ages were intended to suggest how beetle assemblages and associated ecological processes change with time. However, a general lack of accessibility to burns in similar forest-type and altitude in Alberta limited the study to the above two sites.

The Hat Creek burn is *c.* 1,100 ha (Figure 1.2) while the Sheep Creek burn is *c.* 2,400 ha (Figure 1.3). Both were crown fires ignited by lightning and extinguished naturally with minimum human intervention as they are older fires in Alberta. The two study sites contrast strongly with respect to the amount of fire killed wood still apparent on the surface: burned snags and logs are abundant in the Hat Creek area but is not apparent on the soil surface at the Sheep Creek site. However, fireweed (*Epilobium angustifolium* L.), willows (*Salix* species), blueberry (*Vaccinium* species), bog birch (*Betula glandulosa* Michx.) and naturally regenerating lodgepole pine (*Pinus contorta* var. *latifolia* Lamb.) characterize both burned forests.

The overstory of the unburned mature forests surrounding both burns is dominated by never-cut pyrogenic lodgepole pine stands. There is some harvesting activity around the Sheep Creek burn and a number of seismic lines are present in both burns.

Sixteen fire-skips representing a range of sizes were studied (Figures 1.2, 1.3, Table 2). Sub-alpine fir (*Abies lasiocarpa (*Hook.) Nutt.), englemann (*Picea engelmannii* Parry *ex* Engelm.) and black spruce (*Picea mariana* Mill.) dominate the canopy of fire-skips, and species of mosses, bunchberry (*Cornus canadensis* L.*)* and horsetail (*Equisetum* species) characterize the forest floors. Most of the fire-skips are elliptical in shape but a few are roughly triangular. Total areas, lengths and diameters of the fire-skips were determined from 1:15,000 aerial photographs and by on-site measurements.

2.3.3 Tree-Coring

Ages of trees were determined at the Sheep Creek site. The largest trees present in each fire-skip were cored (42 trees in total) and as were in the surrounding forest, ten largest trees each encountered along two transects.

2.3.4 Beetle Trapping

Beetle assemblages were sampled with standard pitfall traps consisting of an outer (1liter) and an inner cup (500 milliliter) that was filled with 2-3 cm of ethylene glycol (silicone free) as a preservative (Spence and Niemelä 1994).

Traps were covered with an elevated (10 x 10 cm) plywood roof to protect them from rain and animal disturbance. Use of pitfall traps as a passive trapping technique has been criticized because it assumes that beetle activity reflects actual abundance (Adis 1979, Halsall and Wratten 1988). However, their use is justified in this study as the trapping technique was standardized across the habitats for comparisons and only whole season catches were analyzed (Baars 1979, Spence and Niemelä 1994).

To sample beetles in the interior of the mature forest and in the burn, six pitfall traps each were placed on three linear transects within the mature forest and on two transects in the burned forest in the 15 year-old study area. In the 36 year-old study site, two transects each were placed in the mature and the burned forest. Traps were spaced 50 m apart to ensure independent sampling and were placed at least 100 m away from any habitat edge (Digweed *et al.* 1995). In the burns, traps were placed at similar distances away from fire-skips. Furthermore, transects in each habitat were separated by more than 150 m.

In each burn, eight fire-skips located more than 100 m from each other and from the mature forest were sampled with traps placed on transects within each skip (Figures 1.2, 1.3). To assess the relationship between beetle richness and skip-area, a variable number of traps were placed at intervals within each fire-skip, depending on the distance of the skip-core from the burn edge. For example, if the skip was 80 m in diameter, then the traps were

placed at 0 (starting at the edge of the skip), 5, 10, 20 and 40 m into the fire-skip (*see* Table 2 for details about traps placed in the skips).

Wildfire created two kinds of natural edges: (1) between the surrounding mature forest and the burn and, (2) between the fire-skip and the burn. To assess beetle distribution patterns in the mature forest and burn edges, two transects each consisting of 11 traps, were placed perpendicularly from the edge (0), and extending 5, 10, 20, 40 and 80 m into both the mature and the burned forest. Before placing traps at the mature forest edge in the highly regenerated 36 year-old burn, trees were cored to determine the ages and hence, the burn-line and placement of the edge trap. To sample beetle activity at the burn edges around eight fire-skips at each study site, traps were placed perpendicularly from the fire-skip edge (0), 5, 10, 20, 40 and 80 m into the burned forest.

Traps were operated continuously during the snow-free period from late June to late/early August and were emptied at *c.* 12 days intervals. Samples were sorted and preserved in 70% ethanol before all adult carabid and staphylinid beetles were identified to the species level (Arnett 1968, Campbell 1968, 1973, 1979, 1982a, 1982b, 1983, 1984, Lindroth 1961-69, Smetana 1971, 1982). Staphylinids of the Subfamily Aleocharinae were excluded from analysis because current systematic work is insufficient and reliable taxonomic keys are unavailable. Reference collections of labeled and identified beetle specimens will be deposited in the next few months at the Strickland Museum, University of Alberta and at the Northern Forestry Centre, Edmonton, Alberta.

2.3.5 Data Analysis

Species diversity patterns for carabid and staphylinid assemblages were estimated using rarefaction (Saunders 1968, Krebs 1989). Rarefaction compensates for differences in sampling effort (e.g., caused by disturbed traps), and can be used as a diversity index as it takes both species richness and abundance into account (Magurran 1988).

Differences in beetle catches in the three habitat types across two burn ages were assessed using a two-way analysis of variance (Abacus Concepts, SuperANOVA 1989). For this purpose, trap catches were pooled over the entire sampling season for each beetle species and standardized to 20 trapping days (the minimum trapping period).

Habitat association patterns for the common (1- 5 % of total catch) and abundant beetle species (> 5 % of total catch) at each study site were determined by calculating the proportion of the average standardized catch in each habitat type: fire-skip, mature forest and burn.

Overall similarity of beetle assemblages in the three habitat types (fire-skips, mature and the burned forest) at the two study sites was analyzed through cluster analysis using the average standardized beetle catch for each habitat type. Clusters within the dendrogram were based on the Bray-Curtis Index for percent similarity with the unweighted group averaging option (Krebs 1989).

CANOCO (Version 3.12) was used to arrange sites along axes, based on carabid and staphylinid species composition by plotting scores for individual traps derived through the ordination process (ter Braak 1991, 1996). For each group, selection of appropriate ordination technique was determined using Detrended Correspondence Analysis (DCA) that tested whether species showed a linear or a unimodal distribution on a hypothetical environmental gradient. Data about carabids fit a linear model as the gradient of the first axis was ≤ 2, and Principal Component Analysis (PCA) was performed. However, due to the presence of 'arch-effect' in the site-score plot, Correspondence Analysis (CA) and later DCA was used to construct the final ordination plot. In contrast, staphylinids fit unimodal distribution pattern. However, because an 'arch-effect' was also present in the site-score plot, DCA was chosen to construct the ordination plot for staphylinids. Site scores for the first two axes with the highest eigenvalues (λ) were plotted and the outermost data-points for each forest type were joined together to construct a two-dimensional ordination space for each habitat type.

Patterns of beetle distribution across the mature forest and burn, and fire-skip and burn edges were assessed by plotting average standardized trap catches of six abundant beetle species. Because beetle catches varied considerably among the traps across the forest edges at both burns, statistical tests were not performed and therefore, only distribution patterns are presented in this paper.

The relationship between the size of sixteen fire-skips and beetle diversity (standardized by rarefaction) was assessed with regression analysis (Minitab Inc. 1995). Similar analyses were also conducted to determine the relationships among fire-skip sizes and total standardized beetle catch and catches of forest beetle species.

2.4 Results

2.4.1 Tree Ages

At the Sheep Creek study site, fire-skips included trees that were, on average, significantly older than those found in the surrounding unburned mature forest ($F = 58.0$, d. f. = 1, 61, $P < 0.001$). A significant, positive relationship between the size of the fire-skips and the oldest tree within the skips, suggested that the largest fire-skips contained the oldest trees on the landscape ($F = 11.7$, d. f. = 1, 7, $P = 0.01$) (Figure 2.1).

2.4.2 Beetle Assemblages

In total, 1,884 carabids and 1,945 staphylinids representing 31 and 32 species respectively, were collected in pitfall traps over two years (Appendices 1 and 2). Eight abundant, eighteen common and thirty-seven rare beetle species (< 1% catch) were collected at the two study sites. Among rare beetles, eleven species were caught only in the habitats in and around the fire-skips.

Rarefaction curves for beetle species accumulation in the fire-skips generally began to level only at the maximum sub-sample sizes, which suggests that beetle assemblages are more diverse than reported in this study (Figures 2.2 and 2.3). At comparable sub-sample sizes, predicted beetle diversities and species accumulation rates were highest in the burned forest, except for staphylinids in the 36 year-old study sites. However, total number of beetle species was highest in the fire-skips again suggesting that these habitats contain speciose assemblages (Appendices 1 and 2).

In the two-way ANOVAs of overall beetle activity, there were no significant differences between different forest types and two ages of the burn for both carabids and staphylinids. However, the 'forest type' X 'age of burn' interaction was significant for carabids ($F = 4.2$, d. f. = 2, $P = 0.03$) but not for staphylinids ($F = 1.6$, d. f. = 2, $P = 0.24$) (Figures 2.4 a, b). Thus, carabid catches in the fire-skips, mature and the burned forest differ, depending on the age of the regenerating burned forest.

A large numbers of beetle species were caught in fire-skips. Almost all the common and abundant beetle species were collected in varying numbers within the skips (Figures 2.5 and 2.6). *Pterostichus empetricola* Dejean, a flightless parthenogenetic species, was collected only in and around the fire-skips (100% catch) at both the study sites. *Calathus ingratus* Dejean, *Elaphrus lapponicus* Gyllenhal, *Mycetoporus americanus* Erichson, *Nebria crassicornis intermedia* Van Dyke, *Olophrum rotundicolle* Sahlberg, *Pterostichus haematopus* Dejean, *Quedius densiventris* Casey and *Tachinus*

frigidus Erichson were found highly associated (65-80% of species catch) with the fire-skips. However, relative proportion of catch for several of these species differed between burn ages. For example, *C. ingratus* was more abundant in the previously burned forest than in fire-skips at the 36 year-old study site. Beetle species such as *C. advena*, *Carabus taedatus* LeConte, *N. crassicornis* and *P. haematopus* that were absent in the younger burn were trapped in the 36 year-old burned forest.

A few species, like *Acidota quadrata* Zetterstedt were found only in fire-skips of the older burn. Also, *Micropeplus laticollis* Mäklin, *Quedius brunnipennis* Mannerheim, *Quedius frigidus* Smetana, *Q. l. labradorensis* Smetana and *Scaphinotus marginatus* Fischer von Waldheim showed somewhat increased association with fire-skips in the older burn. *Eucnecosum brunnescens* J. Sahlberg, *Ischnosoma splendidus* Gravenhorst, *Patrobus foveocollis* Eschscholtz, *Pterostichus riparius* Dejean and *Trechus tenuiscapus* Lindroth were not captured in the mature forest around the older burn, but were associated with both the fire-skips and the burned forest at the 36 year-old study site.

In cluster analysis, the carabid assemblages of mature forests surrounding the two burns clustered together (Figure 2.7 a). Likewise, those of fire-skips in the 15 and 36 year-old study sites had quite similar carabid composition (~ 70% similarity). Assemblages of the 36 year-old burned forest clustered with the fire-skips suggesting beetle movement from the fire-skips to the burned forest. The assemblage of 15 year-old burn was however, less

than 10% similar to those from all other habitat types suggesting that a strong initial effect of fire on carabid species composition persist for some time after wildfire.

The clustering pattern was rather different for staphylinids with the fire-skips in the 15 year-old study site clustering with the two mature forests. In addition, fire-skips and the burn in the 36 year-old study site clustered together (Figure 2.7 b). As with the carabid data, the 15 year-old burn clustered separately but with higher similarity (~30%) to the rest of the forest than observed for carabids.

The DCA ordinations supported results from the cluster analyses. Most of the variation within the forest types was defined by the first axis with an eigenvalue of 0.59 for carabids (Figure 2.8 a) and 0.48 for staphylinids (Figure 2.8 b). In the DCA plot for carabids, the two mature forests as well as the two fire-skips had similar assemblages while the two burned forests had different assemblages. Similarity of carabid assemblages of fire-skips suggest stable habitat conditions. There appears to be a faunal recovery of the 36 year-old burn from both the fire-skips and the mature forest, as the ordination area of the burn overlapped considerably with the fire-skips and the mature forest. In contrast, the staphylinid composition of the 15 and 36 year-old burns were quite similar to each other but those of the fire-skips differed in assemblage composition. In the ordination plots for both carabids and staphylinids, assemblages of the unburned mature forests surrounding each burn overlapped considerably indicating similar species composition.

2.4.3 Beetle Distributions at the Forest Edges

A total of 511 and 1,341 beetles were caught , respectively, at the edges between the mature forest and the burn, and between the fire-skips and the burned forest in pooled data from both study sites (Appendices 1 and 2). More staphylinids were collected at the burn edges around the fire-skips than elsewhere on these landscapes. In the younger burn, *P. riparius* and *Q. labradorensis*, were caught in highest numbers, while in the older burn, *C. advena, S. marginatus, Q. labradorensis* and *Q. brunnipennis* were numerically dominant. Four rare beetle species: *Notiophilus semistriatus* Say, *Harpalus solitaris* Dejean, *Leistus ferruginosus* Mannerheim and *Bolitobius* species, were collected only at the forest edges.

Generally, beetle distributions extended from both the mature forest (Figure 2.9) and the fire-skip (Figure 2.10) edges. At the 15 year-old study site, *N. crassicornis* and *C. advena* were collected primarily in the mature forest with only a few beetles found in the burned forest (Figure 2.9 a). However, *P. haematopus,* and *T. frigidus* had more even distributions across the edge and were collected at least 20 m into the burn. *C. ingratus* was found primarily towards the burned forest, and *Q. densiventris* was collected mainly at the 80m traps on either side of the transects. At the 36 year-old study site, *N. crassicornis* was not collected at the mature forest and burn edge, while *C. advena* was collected up to 20 m into the burn (Figure 2.9 b).

None of the beetle species were collected further than 40 m into the burned forest, suggesting a distribution barrier at the edges around the mature forest at the 36 year-old study site.

At the edges around the fire-skips, similar but somewhat stronger patterns suggestive of beetle recolonization were observed at the 15 year-old study site. Except for *C. advena*, all species were collected in varying numbers in all the traps in the burned forest (up to 80 m from the edge) (Figure 2.10 a). However, at the 36 year-old study site, beetles were generally caught in low numbers around the fire-skips and only *P. haematopus* was collected further than 20 m into the burned forest suggesting more restricted beetle distributions around the fire-skips (Figure 2.8 b). Overall, beetle activity was lower at the 36 year-old study site.

2.4.4 Skip Area and Richness/Activity Relationship

There was no relationship between fire-skip size and overall carabid species richness ($F = 1.37$, d. f. = 1, 15, $P = 0.26$) or activity ($F = 0.03$, d. f. = 1, 15, $P = 0.87$). Similar results were also obtained for the relationship between skip-size and staphylinid species richness ($F = 0.94$, d. f. = 1, 15, $P = 0.36$) and activity ($F = 0.02$, d. f. = 1, 15, $P = 0.90$). However, per trap catches of beetle species such as *N. crassicornis* and *Q. densiventris* were positively related to skip-size as they were caught more often in the larger skips ($F = 10.4$, d. f. = 1, 15, $P = 0.006$) (Figure 2.11).

2.5 Synthesis

2.5.1 Characteristics of Fire-skips

Fire-skips are wet patches of late- successional sub-alpine fir and spruce within a younger pyrogenic lodgepole pine forest. Trees within the fire-skips were on average *c.* 180 years old while those of the surrounding mature forest were only *c.* 72 years old. Thus, these fire-skips have remained unburned through at least one fire-cycle, making them a non-random and a semi-permanent part of the landscape. Such forest patches probably survive wildfire due to a combination of topographic features such as being found in depressions and valleys, and being moist due to high water table level and close proximity to streams (Quirk and Sykes 1971, Rowe and Scotter 1973, Van Wagner 1983).

Age structure of trees in fire-skips varied with skip area. The oldest trees were found in the largest fire-skips, with some of them more than 300 years old. Thus, larger fire-skips are the oldest forest elements on pyrogenic landscapes. Long stand continuity (some more than 400 years), is also characteristic of other spruce stands within temperate forests (Whipple and Dix 1979, Segerström *et al.* 1994, Kneeshaw and Burton 1997, Ohlson *et al.* 1997). In Fennoscandia, these long standing spruce forests have become rare through extensive drainage of wetlands for cultivation and because of the short rotation periods employed in forest harvesting, and their absence on

forest landscapes is thought to be an important conservation problem (Angelstam 1997, Hörnberg *et al.* 1998).

2.5.2 Beetle Assemblages

Fire-skips extend the range of habitats found in younger pyrogenic stands. Their moist character makes them ideal habitats for a large number of beetle species such as *N. crassicornis* and *Q. densiventris. N. crassicornis* has reduced hind wings and therefore has limited dispersal capability, as is true for many temperate carabid forest species (Den Boer 1970, 1990; Spence *et al.* 1996, 1997). Brachypterous beetles are hypothesized to be associated with habitats that are relatively stable and where natural disturbances are rare events (Darlington 1943). However, presence of brachypterous beetle species on these pyrogenic landscapes that are periodically disturbed suggests that fire-skips as long continuos stands are providing relatively stable habitat conditions, and therefore are acting as important faunal sources.

Adults of *N. crassicornis, E. lapponicus* and *Q. densiventris* are strongly hygrophilous (Lindroth 1961 - 69, Smetana 1971). However, larval stages of other species within the genus *Nebria* are known to prefer higher dry ground for pupation (Spence 1979). These contrasting physical characters are well represented in fire-skips by the presence of wet micro-sites such as standing water, and by hummocks and mounds created by fallen trees. Fire-skips are

clearly sufficiently heterogeneous for adult beetles to survive and reproduce. Thus, fire-skips may be vital breeding grounds for these beetle species.

P. empetricola, a high-latitude, brachypterous, parthenogenetic carabid (Lindroth 1961 - 69, Ball 1969, Ball and Currie 1997), was exclusively associated with fire-skips. This study provides the southern most record for this species, which is typical of the western Alaskan tundra. Presence of brachypterous *P. empetricola* only in and around the skips suggests that pockets of wet forest are also significant reserves for some glacial relict beetle species. *P. brevicornis*, another species belonging to the same northern subgenus, *Cryobius*, also has a patchy distribution and is known to be restricted to similar moist, cool forest interiors in the lower lodgepole pine forests (Spence *et al.* 1996). Thus, these two species of this subgenus seem to be highly specialized in habitat-use.

A staphylinid beetle species, *A. quadrata*, known to be restricted to late-successional forests (Spence *et al.* 1997), showed complete association with the fire-skips in the 36 year-old study site. Ten other beetle species *E. brunnescens, I. splendidus, M. laticollis, P. riparius, Q. brunnipennis, Q. frigidus, Q.labradorensis, Q. velox, S. marginatus* and *T. tenuiscapus* also exhibited similar pattern revealing that, as the burned forest regenerates, fire-skips become 'core habitats' for species initially found more widely on the burned landscape. Such patterns are supportive of the 'source-sink hypothesis' (Pulliam 1988, 1996), as fire-skips may be sources for these

beetle populations, and the burn and mature forest may be sink habitats where species extinctions occur periodically.

The ecological importance of wet forest patches similar in age and habitat structure to fire-skips also has become apparent in inventories of spruce swamp forests in Scandinavia. These small patches of forests are rich repositories of rare and endangered vascular plants, bryophytes, fungi and lichens (Söderström 1988, Kuusinen 1996, Ohlson *et al.* 1997, Hörnberg *et al.* 1998). 'Fire-free status, long continuity, stable conditions and richness of ecological niches have all been suggested as features contributing to their high biological diversity' (Hörnberg *et al.* 1998). Another study on wet, spruce-dominated mires in Fennoscandia has shown that *Platynus mannerheimii* Dejean was strongly associated with such habitats, and was adversely affected by clear-cutting activities that alter stand-level characteristics (Niemelä 1996).

Carabid assemblages of fire-skips at the 15 and 36 year-old study sites were similar and dominated by species with limited dispersal ability. Carabid assemblages of the 15 and 36 year-old burned forest differed more because, beetles that became scarce on the landscape after burning had re-established populations in the older burn. In contrast, staphylinid assemblages in the two sets of fire-skips clearly differed from each other and, in fact, only half of the species were shared. Most species of staphylinids have fully functional hind wings, reflecting stronger dispersal ability. Staphylinid assemblages of the fire-skips therefore, may be in a state of flux even 36 years post-fire, with

many species actively colonizing new sites, especially those dependent on patchy and ephemeral sources of food such as mushrooms.

The 15 year-old burn had the most distinct beetle assemblage. A number of beetle species caught in the mature forest and fire-skips were absent or, if present, were restricted to burned areas around fire-skips. Furthermore, the beetle assemblage of the 15 year-old burn was composed primarily of three species, *L. fungicola*, *P. riparius* and *Q. labradorensis*, that were not abundant in either fire-skips or the mature forest. Species generally found in open habitats, such as carabids belonging to the genera *Amara* and *Harpalus* were caught rarely as compared to the activity in clear-cuts in montane lodgepole pine forests (Niemelä *et al.* 1993, Spence *et al.* 1996). These differences suggest either that harvesting creates different landscapes than wildfire, or that there is an established source of these species typical of open-habitats in lower elevation coniferous forests, perhaps due to a longer history of harvesting activity.

2.5.3 Beetle Distributions at the Forest Edges

In contrast to edges created by clear-cutting and agriculture (Baldi and Kisbenedek 1994, Spence *et al.* 1996), natural edges created by wildfire are less abrupt and may not affect distributions of epigaeic beetles. A number of beetle species were collected in varying abundances at the forest edges with *P. riparius* and *Q. labradorensis* as the most abundant species. Generally,

beetle species responded differently to the edges and their distributions were quite patchy.

In the 15 year-old burn, both *N. crassicornis* and *C. advena* were caught only in the mature forest and fire-skips and, except for a few beetles, were not collected in the burned forest. Recently burned forests may not be suitable habitats for survival of some beetle species. In contrast, other species such as *C. ingratus* and *Q. densiventris* were collected up to the limit of trapping (80 m) in the burned forest although the distribution of *Q. densiventris* was quite patchy. At fire-skip edges in the 15 year-old burn, beetle activity was generally higher and most of the beetle species were trapped furthest (80 m) from the skips suggesting active recolonization. A large number of beetles especially staphylinid species, were concentrated around the fire-skips amplifying the role of fire-skips in maintaining faunal assemblages in the fire-origin stands. Presence of different sized and patchily distributed fire-skips in a burned forest may provide suitable habitats for these beetles and thus, may increase landscape connectivity.

Results from the regenerating 36 year-old burn were surprising. Stronger evidence of beetle activity was expected around both edge types, but instead the distribution of beetles, especially at the fire-skip edges seemed more restricted. These differences in patterns could be attributed to year-to-year variation in weather. Total precipitation for the months of June, July and August (sampling period) was 242 mm in 1997, and 144 mm in 1998 (nearly half), while mean growing degree days (base 5° C) were 303 in 1997, and 364

in 1998 (Environment Canada 1997, 1998). Thus 1997, the year in which 15 year-old burn was sampled had a relatively wet, cool summer with shorter growing degree days than the summer of 1998, the year in which the 36 year-old burn was sampled. It is likely that in a wet year such as 1997, beetles that occupy fire-skips would move out into areas around the skips. In contrast, in a dry year like in 1998, connectivity of landscape patches will be seriously constrained as the areas of wet habitats will be smaller and their distribution more patchy.

2.5.4 Skip-Area and Species Richness/Activity Relationship

Fire-skips are relatively isolated patches of forests within a burned matrix and thus resemble insular habitats. However, contrary to predictions of the theory of island biogeography (MacArthur and Wilson 1967), there was no relationship between the fire-skip area and total species richness or abundance. Similar results have been found in studies of ground-dwelling invertebrates in forest remnants created by harvesting (Niemelä *et al.* 1988, Bauer 1989, Davies and Margules 1998, Didham *et al.* 1998). The predictions put forward by island biogeography theory may fail in these harvest-origin landscapes because smaller forest remnants are colonized by species from the surrounding harvested areas (Niemelä *et al.* 1988, Didham *et al.* 1998).

Species-level analysis suggests that larger population of few beetle species such as *N. crassicornis* and *Q. densiventris* existed in larger fire-skips.

As the largest fire-skips contained the oldest trees on the landscape (> 300 years), both species may be associated with specialized microhabitat conditions created by the presence of old trees. Similar association of beetle species with natural elements present in late-successional forests have also been found in other coniferous forests (Heliövaara and Väisänen 1984, Siitonen 1994, Spence *et al.* 1996). It is unclear which long standing attributes are important for *N. crassicornis* or *Q. densiventris*. However, it is likely that populations of these forest beetles will be vulnerable to forest harvesting activities employing a relatively short rotation period (*c.* 100 years) in these high-elevation forests.

2.6 Forestry Considerations

Fire-skips provide important habitats for a number of beetle species, some of them being restricted to these locally stable and moist forests. Fire-skips also promote faunal recolonization by forest beetle species that are concentrated in skips after fire. Thus, harvesting regimes would better emulate natural disturbance by wildfire by leaving a range of different sized forest patches similar in age and structure to fire-skips. Such residual patches would have the potential to act as faunal sources and may enhance the dispersal of forest species and increase landscape connectivity and complexity.

Table 2. Approximate area of the sixteen fire-skips studied and placement of pitfall traps, as dependent on skip width. See Figures 1.2 and 1.3 for relative size and location of fire-skips.

Skip Number *	Area of the Skip (sqm)	Skip Width (m)	Trap Placement (m)
Hat Creek Burn (15 years), studied in 1997			
1	108,000	180	0, 5, 10, 20, 45, 90
2	775,00	150	0, 5, 10, 20, 36, 75
3	1,000	25	0, 5, 8.5,12.5
4	5,950	70	0, 5, 10, 20, 36
5	1,200	20	0, 5, 10
6	3,600	120	0, 5, 10, 20, 40, 60
7	900	30	0, 5, 10, 15
8	600	20	0, 5, 10
Sheep Creek Burn (36 years), studied in 1998			
1	2,106	28	0, 7, 14
2	700	20	0, 5, 10
3	204	12	0, 6
4	448	16	0, 8
5	1,344	30	0, 7.5, 15
6	120	6	0, 3
7	5,250	36	0, 5, 10, 17.5
8	30,000	180	0, 5, 10, 20, 40, 90

* Numbers for fire-skips corresponds to Figures 1.2 and 1.3

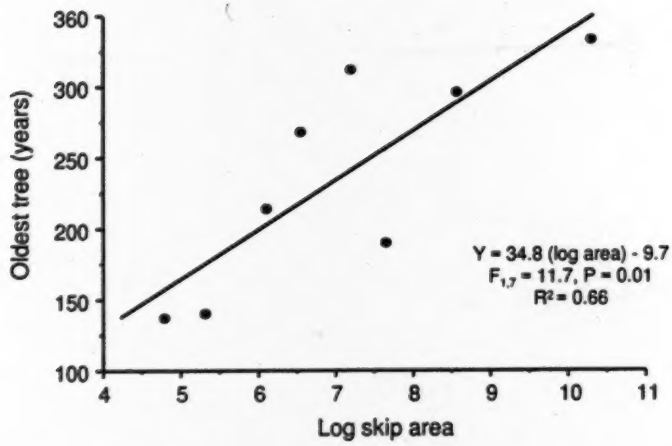

Figure 2.1 . Relationship between the oldest tree in fire-skips and skip area (natural log) at the 36 year-old study site.

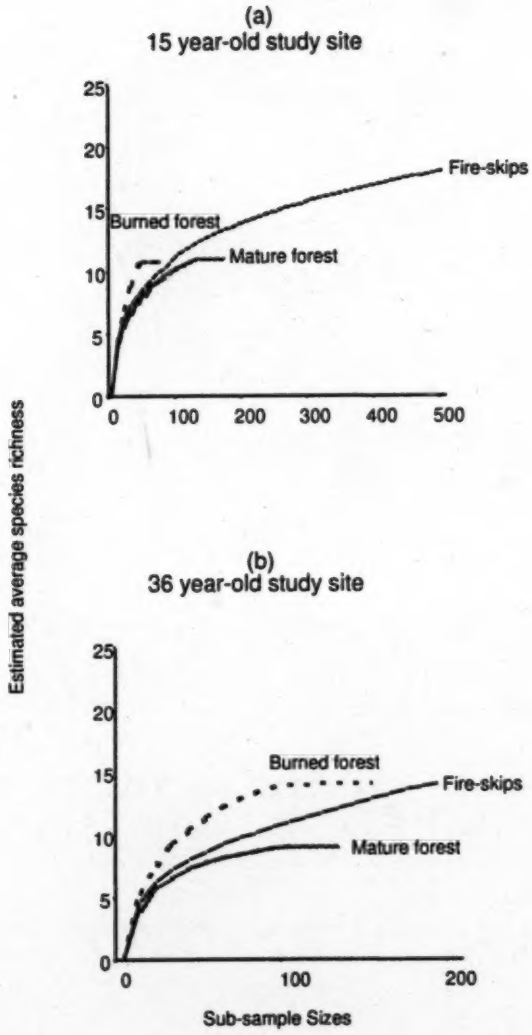

Figure 2.2. Rarefaction diversity estimates of carabid beetles collected in pitfall traps at the 15 (a) and 36 (b) year-old study sites.

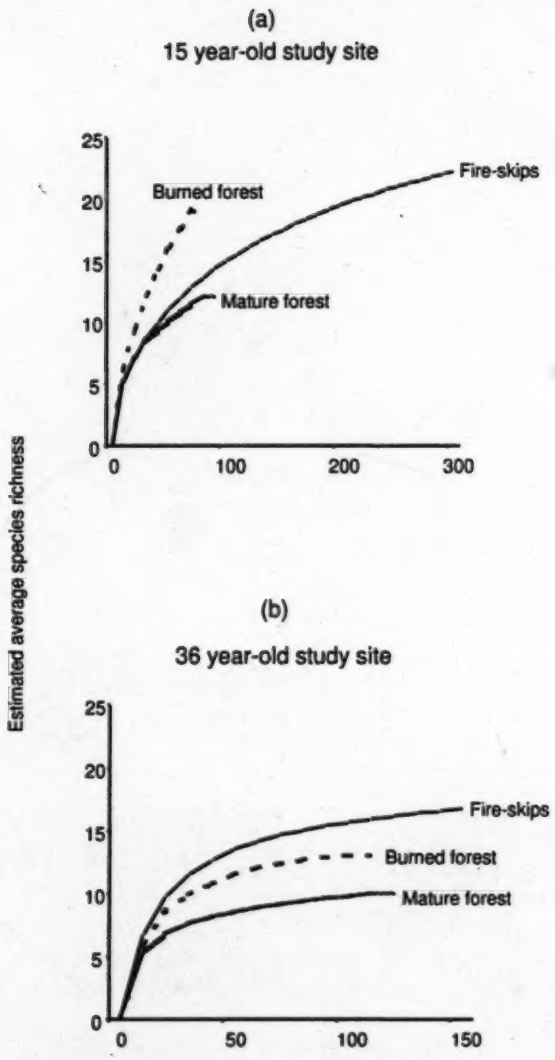

Figure 2.3. Rarefaction diversity estimates of staphylinid beetles collected in pitfall traps at the 15 (a) and 36 (b) year-old study sites.

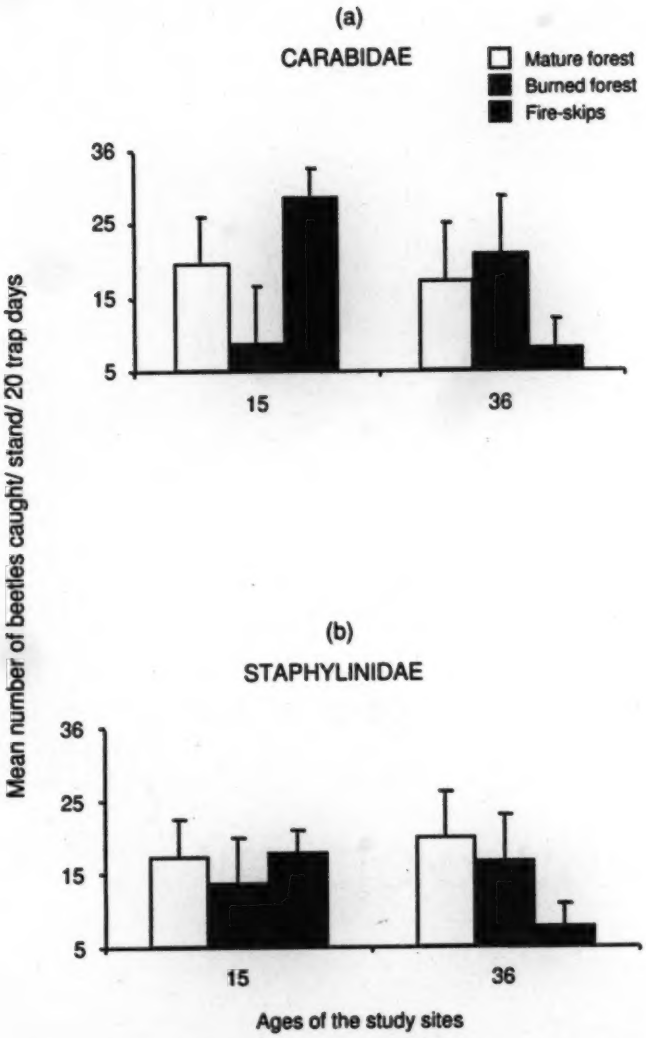

Figure 2.4. Trap catches of carabids (a) and staphylinds (b) in the mature forest, burn and the fire-skips at the 15 and 36 year-old study sites.

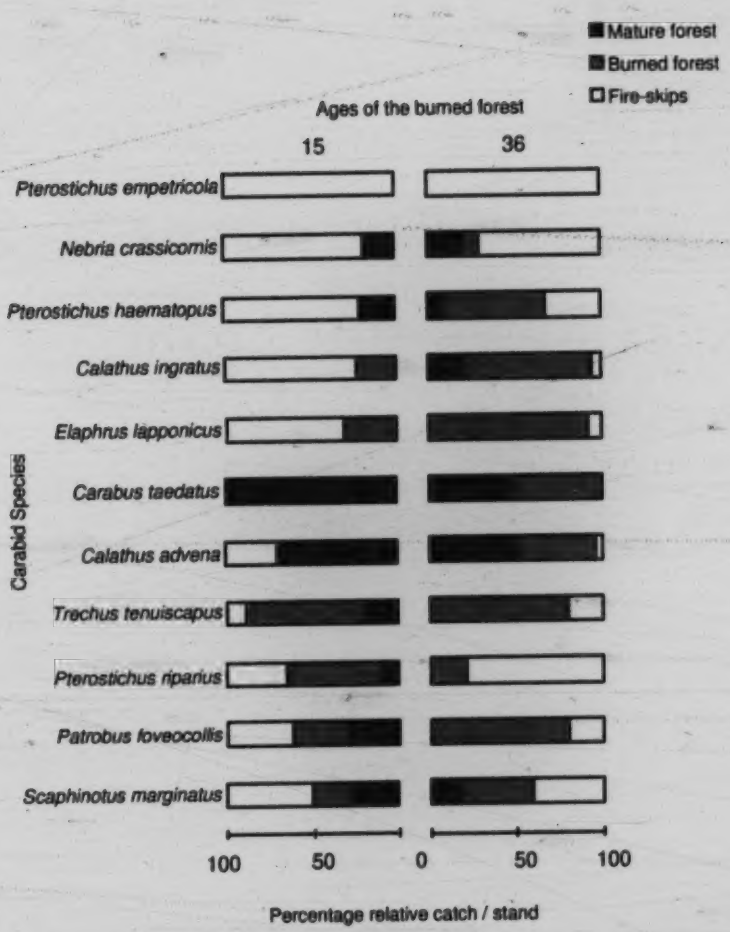

Figure 2.5. Habitat association patterns shown by common and abundant carabid species caught in pitfall traps at the 15 and 36 year-old study sites.

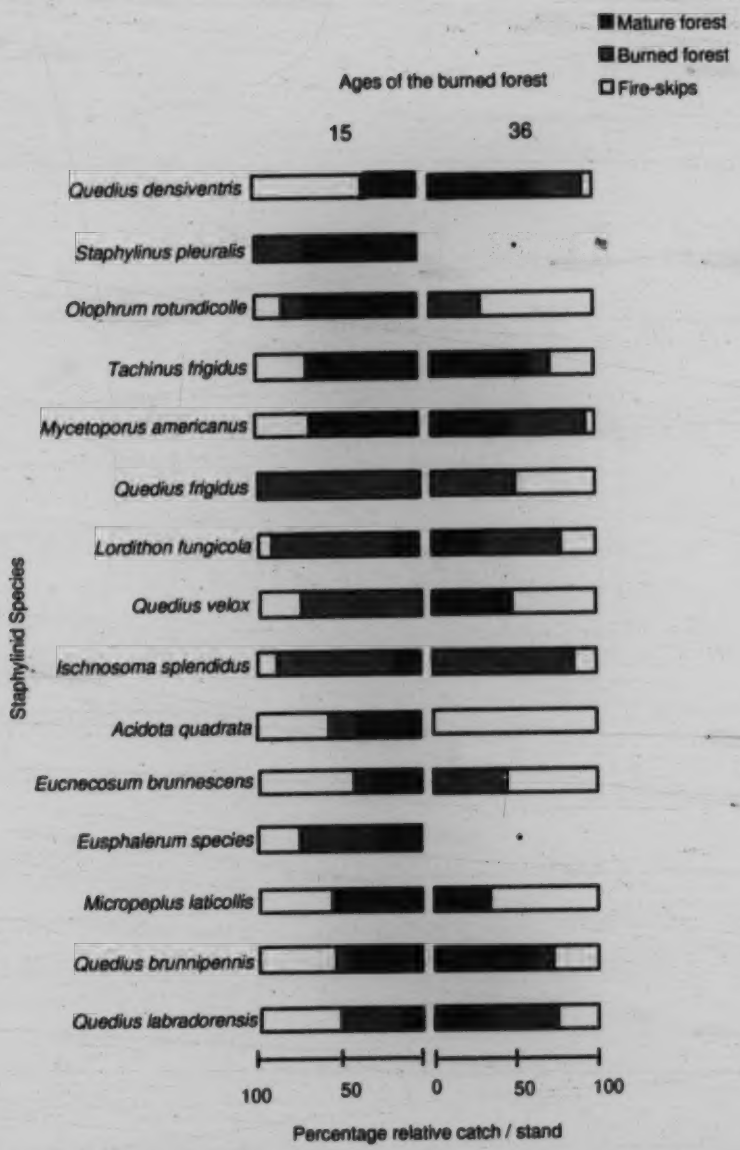

Figure 2.6. Habitat association patterns shown by common and abundant staphylinid species caught in pitfall traps at the 15 and 36 year-old study sites. An asterisk denotes that the species is absent.

Figure 2.7. Cluster analysis of Bray-Curtis similarity measure of carabid (a) and staphylinid (b) assemblages caught in fire-skips, mature forest and burn at the 15 and 36 year-old study sites.

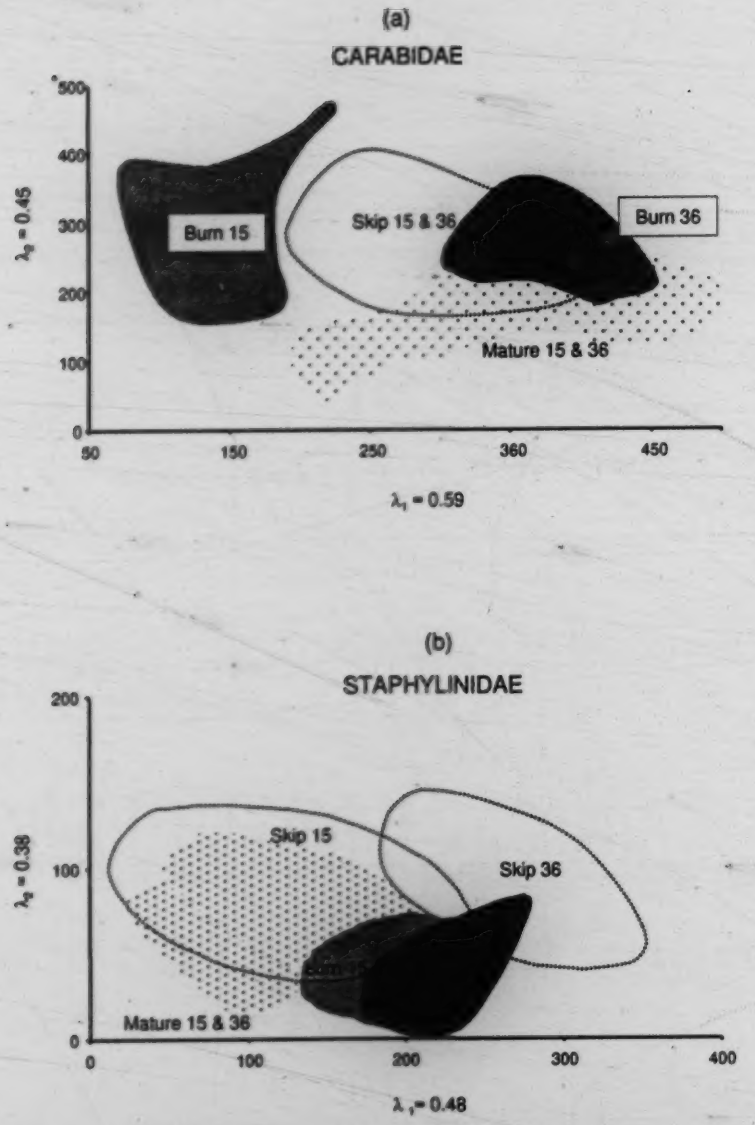

Figure 2.8. Detrended Correspondence Analysis (DCA) sample score plots of carabid (a) and staphylinid (b) assemblages in the mature forest, burn and fire-skips at the 15 and 36 year-old study sites.

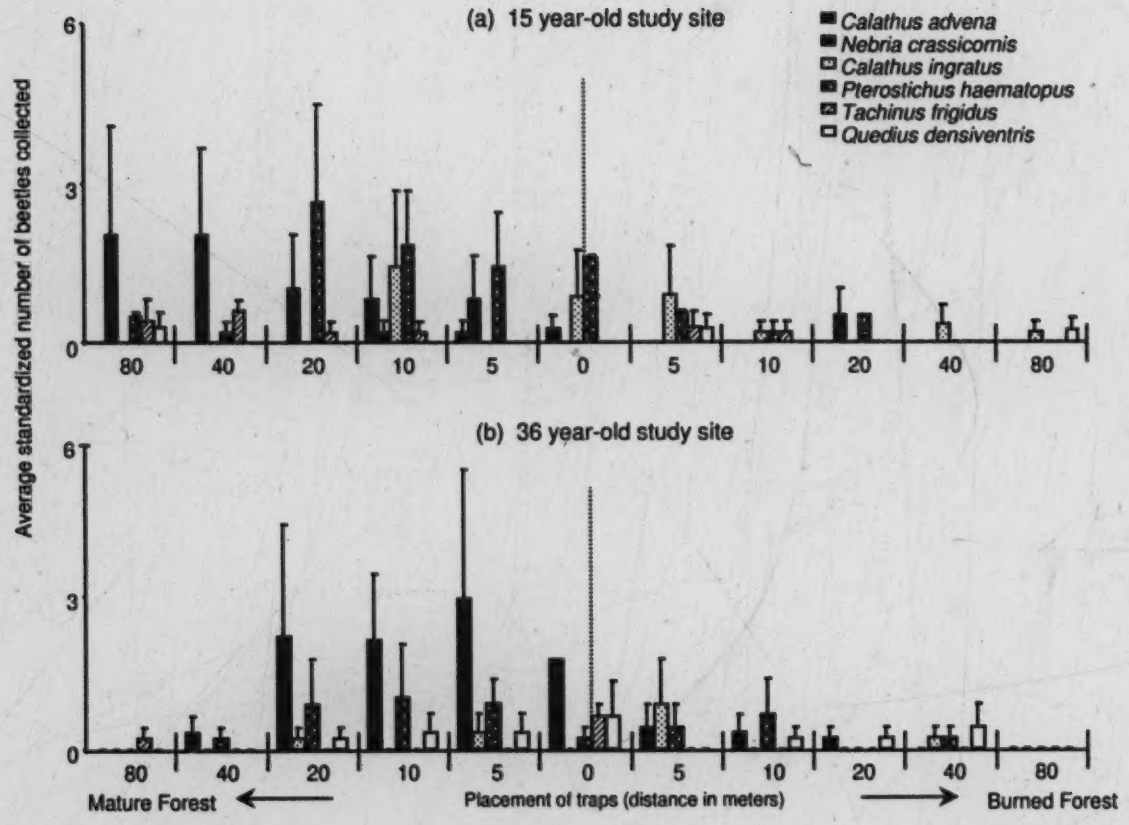

Figure 2.9. Distribution patterns of six beetle forest species at the forest edges between mature forest and the burn.

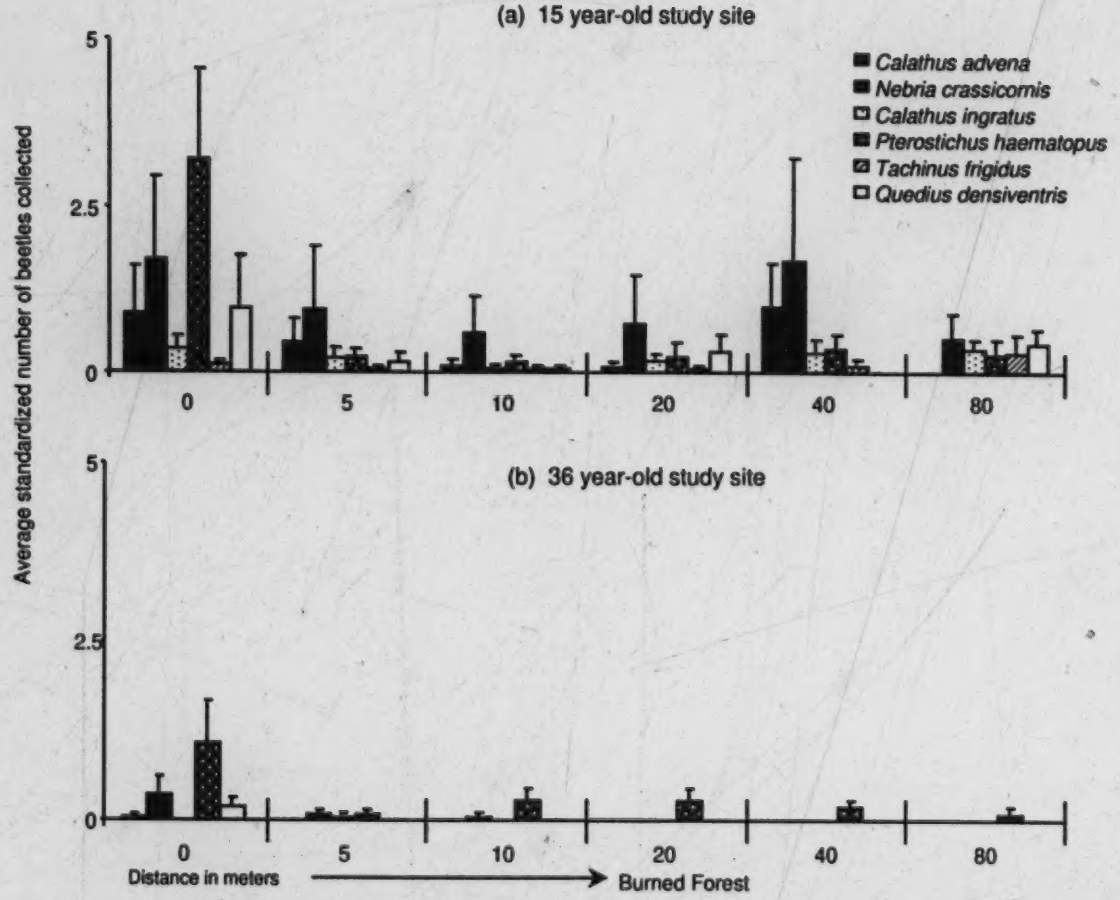

Figure 2.10. Distribution patterns of six forest beetle species at the forest edges between fire-skips and the burn.

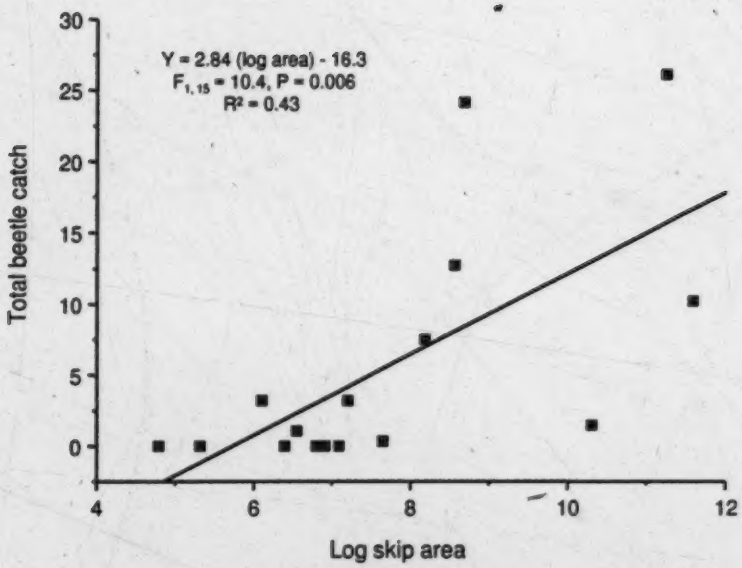

Figure 2.11. Relationship between catches of *Nebria crassicornis* in fire-skips and fire-skip sizes.

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Chapter 3 . Influence of Forest Heterogeneity on Epigaeic Beetles

3.1 Synopsis

Relationships among diversity and catches of litter-dwelling beetles (Coleoptera: Carabidae, Staphylinidae) and attributes of forest heterogeneity were studied in fire-origin stands. Total catches and richness of beetles were correlated primarily with overstory diversity (forest composition), but a number of beetle species were also correlated with understory diversity suggesting the importance of both undergrowth and canopy composition as factors in beetle habitat associations. Variables of forest structure characterized by amount of mosses, grasses, forest canopy, undergrowth plants and coarse-woody debris were significantly correlated with beetle catches and diversity. Relationships among spatial distribution of beetles and forest attributes varied within similar forest types and across forest ages suggesting that micro-sites created by specific combinations of forest attributes were important for beetle assemblages. Results underscore the importance of environmental factors in regulating litter-dwelling beetle assemblages at small scales within pyrogenic landscapes.

3.2 Introduction

Spatial and temporal heterogeneity are inherent characteristics of forested ecosystems (Wiens 1989, Kareiva 1990). Heterogeneity on several scales influences ecological processes such as population dynamics and

interspecific interactions (Huffaker 1958, MacArthur and MacArthur 1961, Pianka 1967, Recher 1969, Den Boer 1981, Kareiva 1990), and may provide a background for modeling life history strategies (Southwood 1977, 1988). Origin, scale, definition and quantification of heterogeneity have been much discussed (Addicott *et al.* 1987, Turner 1987, Wiens 1989, Kotlair and Wiens 1990, Kolasa and Pickett 1991, Dutilleul and Legendre 1993, Li and Reynolds 1995, Roos and Sabelis 1995), and now heterogeneity *per se* is increasingly recognized as an important force structuring faunal assemblages.

In boreal and montane forests, landscape heterogeneity is primarily generated through natural disturbances, such as wildfires (Hunter 1993, Haila *et al.* 1994, Bunnell 1995). These disturbance events re-occur every 80-100 years (Strong 1992) and result in complex mosaics of differently aged forests and stand types. For example, in montane coniferous forests in western Canada, a typical landscape mosaic consists of unburned residual patches of late-successional spruce (*Picea engelmannii* Parry *ex* Engelm., *Picea mariana* Mill.) and fir (*Abies lasiocarpa* (Hook.) Nutt.), many of which originated as 'fire-skips', within a matrix of younger lodgepole pine (*Pinus contorta* var. *latifolia* Lamb.) stands (*see* Chapter 2 for details).

Influence of key-habitat attributes such as forest architecture, composition, etc., on the dynamics of many biological populations are little understood within forests, and significant gaps in knowledge of the ecological roles of above-ground structure and woody debris are recognized (Spies 1998). Therefore, I examined relationships among forest heterogeneity and

two invertebrate assemblages representing the forest floor fauna in three different forest types within pyrogenic stands.

3.3 Methods

3.3.1 Study Organisms

Studies of the interaction of arthropods and habitat heterogeneity in the past have focused primarily on phytophagous groups (Southwood *et al.* 1979, Brown and Hyman 1986), and studies of predatory and other trophic groups are lacking (Buse 1988). Among predatory groups, carabid beetles (Coleoptera: Carabidae) were chosen for this study because they are generally non-randomly distributed with respect to micro-habitats (Thiele 1977, Luff 1986, Niemelä 1990, Niemelä *et al.* 1992 a), and in addition to interspecific interactions, are clearly influenced by habitat configurations (Den Boer 1981, Szyszko 1986, Buse 1988). Although staphylinid species (Coleoptera: Staphylinidae) tend to be less specialized with respect to habitat affinity, they represent a greater range of feeding types and also respond to changes in environment quality (Buse and Good 1993).

3.3.2 Study Sites

The study was conducted in sub-alpine (1,525 - 1,700 m) coniferous forests of the northern Rocky Mountains (Figure 1.1). The sites are specifically located in the Weyerhaeuser Forest Management Area north of

Grande Cache in western Alberta, Canada. The Hat Creek Fire (54° 1391' N 119° 4215' W), burned in 1982 (a 15 year-old burn) (Figure 1.2), and the Sheep Creek Fire (54° 055' N 119° 10' W), burned in 1961 (a 36 year-old burn) (Figure 1.3). The younger burn (*c.* 1,100 ha) was sampled in 1997 and the older burn (*c.* 2,400 ha) in 1998. Three different biotopes (fire-skips, mature and burned forest) were studied at two burns to assess whether habitat association patterns are consistent on landscapes with different disturbance history.

The two study sites contrast markedly with respect to the amount of fire killed wood still apparent on the surface: burned snags and logs are abundant in the Hat Creek area but is not apparent on the soil surface at the Sheep Creek site. However, fireweed (*Epilobium angustifolium* L.), willows (*Salix* species), blueberry (*Vaccinium* species), bog birch (*Betula glandulosa* Michx.) and naturally regenerating lodgepole pine characterize both burned forests.

3.3.3 Beetle Sampling

Epigaeic beetles were sampled with standard pitfall traps consisting of an outer cup (1 liter) that held an inner cup (500 milliliter) filled with 2-4 cm of ethylene glycol as a preservative and a killing agent (Spence and Niemelä 1994). A plywood roof was suspended over each trap to minimize flooding and disturbances by wild mammals. At the 15 year-old study site, six pitfall traps, each separated by 50 m, were placed on three linear transects in the

interior of the mature forest and on two transects in the burned forest. However, at the 36 year-old study site, two transects each consisting of six pitfall traps were placed in both the mature and burned forest. Eight fire-skips at each study site were sampled with transects placed at the edge of the fire-skip (0 m) and extending perpendicular to the core of the skip. Number of traps placed in each fire-skip varied depending on the width of the skip (Table 2).

To ensure independent samples, traps were spaced at least 100 m from any edge habitat, and transects were separated by more than 150 m (Digweed *et al.* 1995). Fire-skips selected for sampling were more than 100 m away from each other and from the surrounding unburned forest. In the burns, traps were placed at similar distances away from the fire-skips.

Trapping was conducted continuously starting in early/ late June to August, roughly the snow-free period in these sub-alpine forests. Samples were collected periodically at two-week intervals, and were sorted, labeled and preserved in 70% ethanol. All adult carabids and staphylinids collected in two years were identified to species using available literature (Arnett 1968, Campbell 1968, 1973, 1979, 1982a, 1982b, 1983, 1984, Lindroth 1961-69, Smetana 1971, 1982). Staphylinids of the Subfamily Aleocharinae were excluded from analysis because current systematic work is insufficient and reliable taxonomic keys are unavailable. A reference collection of labeled and identified beetle specimens will be deposited in the next few months at the

Strickland Museum, University of Alberta and in the Northern Forestry Centre, Edmonton, Alberta.

3.3.4 Vegetation Sampling

Aspects of habitat heterogeneity were assessed for fire-skips, mature and burned forest at both study sites using a protocol modified from Niemelä and Spence (1994). Vegetation plots (3.5 X 3.5 m) were established centered on each pitfall trap. All plant species in each plot were identified using Moss and Packer (1992) and Johnson *et al.* (1995). Most plants were identified in the field but some were brought back to the laboratory and identified using reference material at the Plant Herbarium at the University of Alberta, Edmonton. A number of species groups include hybridizing species such as those belonging to the Genus *Salix* could not be reliably separated and were therefore, placed together as a single taxon.

Percentage cover was categorized for each plant species as: 0 = absent (0%), 1 = rare ($\leq$ 1%), 2 = common (1.1-20%), and 3 = abundant (>20%). These categories were used because subtle differences among small cover values are of greater significance than similar differences among high cover values (Causton 1988). Tree cover was determined by counting the numbers of standing trees and those with branches overhanging the plot.

Shrub density was recorded as the number of times a 0.5 m high stick intersected a shrub stem on both the North-South and East-West transect

through the plot. Percentage cover of mosses and lichens was also recorded. Amount of coarse-woody debris was estimated by counting the total number of snags and logs more than 5 cm diameter present within vegetation plots.

3.3.5 Statistical Analysis

To determine possible relationships among total number of understory and overstory species (forest composition) and measures of total beetle catches, activity of common and abundant species, diversity and dominance, step-wise multiple regressions were performed (Abacus Concepts, StatView 1992). Beetle catches for pitfall traps were standardized to 20 trapping days to account for disturbed traps.

A number of diversity indices were used to describe beetle assemblages. Beetle diversity per trap was estimated by total number of beetle species (S) and Shannon-Weiner Index of diversity (H') (Appendix 3) (Magurran 1988). The Shannon-Weiner index derived from information theory, is based on the assumption that all species are equally represented in the sample (Pielou 1975). Two types of dominance indices, Berger-Parker (d') and Simpson's index (S'), that measure species diversity with emphasis on abundant species, were calculated per trap. The Berger-Parker index is the inverse of the catches of the most dominant species in a sample divided by the total catches in the sample (Magurran 1988). The Simpson's index is based on the sum of probabilities that two randomly chosen individuals are

conspecific with respect to each species in the sample (sensu Kikkawa, 1986). To ensure that the indices increased with increasing diversity and decreased in dominance, reciprocal forms of the dominance measures were used in the analysis (Magurran 1988). Diversity indices were calculated from spreadsheets using MS Excel software (Version 7).

To assess relationships among forest structure and beetle activity and diversity, vegetation in each plot was divided into structural types as follows: (1) forest canopies constituted mature trees taller than 10 m; (2) coniferous shrubs were immature trees less than 10 m in height; (3) multi-stemmed plants were woody shrubs less than 10 m tall; (4) single-stemmed plants constituted plants with a single, erect stem; (5) forest-floor plants were plants with low growth forms less than 50 cm in height; and (6) plants that formed mats included those that forming aggregations low on the forest floor (Moss and Parker 1992, Johnson *et al.* 1995) (Appendix 4). Within each category, rank-abundance of each attribute was pooled for analysis. Data on shrub-cover, mosses, lichens, grasses, snags and logs were also included as individual variables in the regression models. Since, shrub-cover, forest canopy, snags and logs were recorded as numbers per trap, data were converted to percentage relative cover on the landscape, and then transformed to the ordinal scale. Step-wise multiple regressions were used to determine whether some combinations of these twelve independent variables in forest structure were significantly correlated with standardized total catches (log-transformed when necessary), catches of common and abundant beetle, species diversity

(total number of species, Shannon-Weiner index) and dominance measures (Berger-Parker index, Simpson's index).

In an effort to spread the range of independent variables, I also conducted stepwise multiple regression analyses for each burn using pooled data over the three forest types. Results are not presented in this paper because regression relationships partitioned by forest type were generally more useful in understanding relationships among habitat heterogeneity and beetle distribution patterns.

3.4 Results

A total of 1,081 carabids and 896 staphylinids representing 28 and 31 species, respectively, were collected in two years of sampling (Appendices 1 and 2, exclude beetle catches at the forest edges). Overall, forty-one undergrowth plant species were used to characterize the undergrowth vegetation, while four tree species comprised the forest canopy around the trap sites (Appendix 4).

3.4.1 Forest Composition

Total beetle catches at the two study sites were not correlated with understory diversity. Total beetle catches, diversity and dominance measures in some forest types were however, either positively or negatively correlated

with overstory diversity suggesting that composition of forest canopy was a more important correlate of beetle distribution patterns.

Activity of most common and abundant beetle species was, however, correlated with both understory and overstory diversity, as observed in the mature forest at the two study sites (Table 3.1). In the 15 year-old burn, none of the beetle species showed any habitat associations, but in the highly regenerated 36 year-old burn, knowledge of attributes characterizing forest composition were positively correlated with catches of beetle species. Beetle catches were exclusively related to overstory diversity in fire-skips at both study sites.

3.4.2 Forest Structure

3.4.2.1 Determinants of Beetle Catches

Overall, beetle activity and diversity were correlated with most of the twelve variables characterizing forest structure, thus reflecting the importance of habitat attributes. Individually, these variables accounted for 5 - 90% of the variation in beetle distributions. Total beetle catches were significantly correlated with six stand structure variables including, cover-abundance of forest canopy, single-stemmed plants, forest floor plants, mosses, grasses and snags, that were characteristically present or absent from the respective forest types. (Table 3.2). The most common correlates with beetle catches were grass and snag cover.

Species-level analysis indicated that almost all the variables of forest structure in fire-skips, mature and burned forest were positively or negatively correlated with catches of common and abundant beetle species (Tables 3.3 - 3.8). Catches of beetles were correlated with different combinations of structure variables and most species exhibited different microhabitat affinities. For example, in the mature forest surrounding the younger burn (Table 3.3), catches of *Trechus tenuiscapus* Lindroth were positively correlated with grasses and mosses, and negatively correlated with undergrowth plants forms that shade the forest floor, while in the older burn (Table 3.6), this species showed positive associations with plants with single stems. Also, patterns of habitat association for most beetle species varied across study sites suggesting that microhabitat variation is important for beetles at a relatively small scale.

3.4.2.2 Determinants of Beetle Diversity

Diversity of beetles was correlated with coarse-woody debris, forest canopy, grasses, coniferous plants, lichens, plants that formed mats and single-stemmed plants (Tables 3.9 and 3.10). Coarse-woody debris and plants with single-stems were the most common significant variables. Diversity of the most abundant species as determined from dominance measures, were correlated with all the variables of forest structure except shrub-cover (Tables 3.11 and 3.12). However, both diversity and dominance indices generally provided different association patterns of beetles reflecting

inherent variability. Overall, more than half of the beetle associations were negative, suggesting that higher number of species was not always related to greater structural heterogeneity on the landscape.

3.5 Synthesis

3.5.1 Forest Composition

Positive relationships are generally found between the diversity of phytophagous arthropods (for example, those belonging to the suborder Homoptera), and plant species because arthropods may respond to higher abundance of specific host plants (Murdoch *et al.* 1972, Duffey *et al.* 1974, Tscharntke and Greiler 1995). Buse (1988) also reported positive correlations between the diversity of polyphagous predators such as carabid beetles and plants although the basis for this is harder to explain. Such relationships may exist because more complex plant communities provide a greater range of micro-habitats or potential prey species (Dennis *et al.* 1997).

Significant relationships among understory and overstory diversity, and dominance measures and total activity were, however, absent in this study. Instead, catches of some beetle species in pyrogenic stands were correlated with the diversity of overstory suggesting that habitat elements created as a result of a diverse forest canopy may be more important in influencing the structure of beetle assemblages than is composition of the undergrowth foliage, under which these beetles actually live. Litter-dwelling beetles may

not be responding directly to vertical heterogeneity *per se*, as has been observed in bird, mammal and epiphytic lichen communities (Currie 1991, McCune *et al.* 1997), but rather to other attributes such as increased shading effects or variable characteristics of soil litter present in diverse forest stands.

Catches of most of the common and abundant beetle species were however, correlated with both understory and overstory diversity (Table 3.1). In the younger burn, none of the variables of forest composition were correlated with beetle catches, but in the older burn, a number of variables were correlated with catches of a number of beetle species such as *Carabus taedatus* LeConte, *Olophrum rotundicolle* Sahlberg and *Pterostichus haematopus* Dejean. This may reflect regeneration of the burn and increased cover-abundance of both understory and overstory species, leading to increased recolonization (*see* Chapter 2) and opportunity for associations shown by beetle species.

In the fire-skips at the two study sites, only diversity of forest canopy was correlated with catches of beetle species such as *Calathus ingratus* Dejean, *Eusphalerum* species, *Ischnosoma splendidus* Gravenhorst, *Patrobus foveocollis* Eschscholtz and *Scaphinotus marginatus* F. von Waldheim. Possibly beetles may be correlated with higher diversity of habitat attributes created as a result of higher tree diversity, or that some species, for example, *C. ingratus*, may associate primarily with spruce and fir trees characteristically present within the fire-skips.

3.5.2 Forest Structure

I elaborate on the following general points that emerged from overall analysis of forest structure. First, forest structure was clearly an important correlate of beetle catches and diversity. At both study sites, structural attributes reflected in amount of coarse-woody debris, forest canopy, undergrowth, lichen, moss, grass and shrub cover were significantly correlated with beetle catches and diversity (Tables 3.2 - 3.12). Interestingly, within any forest type, no single variable could be isolated as the single most important factor regulating beetle species. In some forests, combinations of a number of factors were correlated with beetle distributions. This implies that beetles may be associated with a suite of variables characterizing structure, and with resulting micro-sites existing within forested ecosystems.

Overall, results from this study are consistent with those of other studies of beetles, especially carabids, in which preferences for certain micro-habitats have been documented (Goulet 1974, Thiele 1977, Buse 1988, Niemelä and Spence 1994). Such relationships are hypothesized because the structure of habitats may determine micro-spatial gradients, thereby influencing prey availability, inter-specific interactions or predation rates (Hengeveld 1985, Loreau 1986, Buse and Good 1993, Niemelä and Spence 1994). Beetles may also respond directly to abiotic conditions such as light, temperature and moisture gradients (Thiele 1977), that may be created and maintained by physical aspects of vegetation structure, for example fallen woody debris.

In contrast to the 'habitat heterogeneity hypothesis' that predicts that faunal diversity should increase with greater structural heterogeneity (Whittaker and Levin 1977, Hart and Horwitz 1991), diversity of epigaeic beetle assemblages was generally negatively correlated with variables associated with structural heterogeneity (Tables 3.9 - 3.12). None of the variables were correlated with the diversity of either carabids and staphylinid beetles in a number of habitats of a burned boreal landscape. Thus, greater heterogeneity *per se*, or availability of more habitats, did not reflect higher occupancy rate by beetle species. These results imply that factors other than vegetation may influence epigaeic beetles. Unmeasured variables such as soil depth or moisture (Thiele 1977), that may influence larval stages that burrow into soil, may also thereby determine adult beetle distributions. Composition of beetle assemblages may also be determined by inter-specific interactions (Loreau 1986, 1990) such as competition and predation, and at larger spatial and temporal scales, colonization or dispersal rates may play crucial roles in determining extant distribution of species (Ricklefs 1987, Ricklefs and Schluter 1993).

Variation in habitat associations within forests was also quite high between the two study sites. Beetles may be associated with different vegetation characteristics in apparently quite similar forests, such as mature forest and fire-skips. High variability in associations is to be expected in the burned forest but seems puzzling in the mature forest and fire-skips because

with canopy closure, conditions on forest ground should become more stable and similar (Niemelä *et al.* 1996).

Most of the structural attributes that were correlated with beetle catches were characteristic of the respective forest patches. To illustrate, in the 15 year-old burn, carabid catches were positively correlated with grass cover, while in the fire-skips, catches were positively correlated with forest canopy (Table 3.2). Fir and spruce accounted for the fire-skip canopy and therefore, populations of beetle species such as *P. haematopus*, that were numerically dominant in skips, would be expected to be associated with the structural attributes present within the fire-skips, where as catches of species primarily caught in burned forests such as *T. tenuiscapus*, would be associated with grasses that grew abundantly in the burned forest (Johnson *et al.* 1995). Indeed, species-level analysis revealed that in the mature forest *T. tenuiscapus* was positively associated with grasses and mosses in open areas, and negatively associated with undergrowth plant forms that shade the forest floor (Table 3.3).

Ranges of cover-abundance of various attributes of forest structure may also explain patterns of beetle associations. For example, in the 15 year-old burn, total beetle catches were positively correlated with grasses, but in the 36 year-old burn, beetle catches were negatively correlated with snags (Table 3.2). In the younger burn, grasses were abundant (20 - 100% cover) and beetle species present in higher numbers in the burn such as *Pterostichus riparius* Dejean and *Lordithon fungicola* Campbell would be expected to show

positive associations (Table 3.5). However, in the older burn, snags were generally absent or when present were rare (0 – 1% cover). Possibly beetle species may be perceiving snags as obstructions for movement whenever they were present and therefore, showed negative associations.

Thus, to conclude, diversity and activity of forest beetles were significantly correlated with attributes characterizing composition and structure of the forest. However, as has been suggested in studies on ground beetles in coniferous forests in Finland (Niemelä *et al.* 1986), in heathlands in Britain (Gardner 1991), and in deciduous forests in central Alberta (Niemelä and Spence 1994), local distributions and diversity of beetles may also be regulated by other ecological processes, and across several spatial scales. This emphasizes the subtle interplay of local and regional factors in maintaining the spatial distribution of epigaeic beetles on natural landscapes.

Table 3.1. Relationships between understory (U) and overstory (O) diversity and common and abundant beetle species ($P < 0.05$, $R^2 = 0.10 - 0.90$). '+' and '-' refers to positive and negative relationships respectively.

		15 year-old burn			36 year-old burn		
Taxa	Species	Mature	Burn	Skips	Mature	Burn	Skips
Carabidae	*Calathus advena*						
	Calathus ingratus			+O			
	Carabus taedatus	+U				+O	
	Elaphrus lapponicus						
	Nebria crassicornis	+U					
	Patrobus foveocollis			+O			-O
	Pterostichus empetricola						
	Pterostichus haematopus					+O	
	Pterostichus riparius	+U					
	Scaphinotus marginatus			+O	+U, -O		
	Trechus tenuiscapus	-U					
Staphylinidae	*Acidota quadrata*						
	Eucnecosum brunnescens						
	Eusphalerum species			-O			
	Ischnosoma splendidus						-O
	Lordithon fungicola						
	Micropeplus laticollis				-O		
	Mycetoporus americanus						
	Olophrum rotundicolle	-O				+U	
	Quedius brunnipennis	-O			-U	+U	
	Quedius densiventris				-U		
	Quedius frigidus					+U	
	Quedius labradorensis	-O			+U		
	Quedius velox						
	Staphylinus pleuralis	-O					
	Tachinus frigidus						

Table 3.2. Stepwise multiple regression models for predicting epigaeic total beetle catches from forest structure.

Taxa	Study Sites	Forest Types	Model	Adjusted R^2	F	P
Carabidae	15 year-old burn	Mature forest	0.24 + 0.66 (Forest Floor Plants)	0.44	14.34	0.002
		Burned forest	- 6.05 + 2.31 (Grasses)	0.78	39.08	< 0.001
		Fire-skips	1.7 + 2.44 (Forest Canopy)	0.10	4.77	0.04
	36 year-old burn	Mature forest	1.77 + 2.74 (Snags)	0.49	11.34	0.007
		Burned forest	1.07 - 5.68 (Snags)	0.77	37.56	0.001
		Fire-skips	- 4.71 + 1.21 (Mosses) + 0.25 (Single-stemmed plants)	0.36	7.21	0.004
Staphylinidae	15 year-old burn	Mature forest	1.39 + 1.4 (Grasses)	0.22	5.89	0.03
		Burned forest	*	*	*	*
		Fire-skips	1.29 - 8.85 (Grasses)	0.11	5.36	0.03
	36 year-old burn	Mature forest	*	*	*	*
		Burned forest	*	*	*	*
		Fire-skips	1.96 - 1.76 (Snags) - 0.98 (Forest Canopy)	0.30	5.88	0.009

* refers to no independent variable being significant

Table 3.3. Relationships between common and abundant beetle species and variables in forest structure in mature forest at the 15 year-old study site. '+' and '-' refers to positive and negative relationship respectively. Forest structure abbreviations: FC = Forest Canopy, CS = Coniferous Shrubs, SH = Shrubs, SP = Plants with Single Stems, FP = Forest-floor Plants, PM = Plants that form Mats, MO = Mosses, LI = Lichens, SN = Snags, LO = Logs, SC = Shrub-cover

Taxa	Species	FC	CS	SH	SP	FP	PM	GR	MO	LI	SN	LO	SC
Carabidae	*Calathus advena*							-					
	Calathus ingratus												
	Carabus taedatus										+		
	Elaphrus lapponicus												
	Nebria crassicornis							-					
	Patrobus foveocollis	+		+									
	Pterostichus empetricola												
	Pterostichus haematopus	+											
	Pterostichus riparius							+					
	Scaphinotus marginatus	+											
	Trechus tenuiscapus		-				-	+	+				
Staphylinidae	*Acidota quadrata*			+									
	Eucnecosum brunnescens						-						
	Ischnosoma splendidum												
	Lordithon fungicola												
	Micropeplus laticollis												
	Mycetoporus americanus												
	Olophrum rotundicolle	-										-	
	Quedius brunnipennis							+					
	Quedius densiventris				-								
	Quedius frigidus												
	Quedius labradorensis					-		+					
	Quedius velox												
	Staphylinus pleuralis							+					
	Tachinus frigidus					+							

Table 3.4. Relationships between common and abundant beetle species and variables in forest structure in mature forest at the 36 year-old study site. '+' and '-' refers to positive and negative relationship respectively. Forest structure abbreviations: FC = Forest Canopy, CS = Coniferous Shrubs, SH = Shrubs, SP = Plants with Single Stems, FP = Forest-floor Plants, PM = Plants that form Mats, MO = Mosses, LI = Lichens, SN = Snags, LO = Logs, SC = Shrub-cover

Taxa	Species	FC	CS	SH	SP	FP	PM	GR	MO	LI	SN	LO	SC
Carabidae	*Calathus advena*										+		
	Calathus ingratus												
	Carabus taedatus								-				
	Elaphrus lapponicus												
	Nebria crassicornis										+		
	Patrobus foveocollis												
	Pterostichus empetricola												
	Pterostichus haematopus			-									
	Pterostichus riparius												
	Scaphinotus marginatus	-		+	+								
	Trechus tenuiscapus												
Staphylinidae	*Acidota quadrata*												
	Eucnecosum brunnescens												
	Ischnosoma splendidus												
	Lordithon fungicola	+						-	-			-	
	Micropeplus laticollis	-											
	Mycetoporus americanus	-		-	-		-		-	-	-		
	Olophrum rotundicolle												
	Quedius brunnipennis												
	Quedius densiventris				-					-			
	Quedius frigidus												
	Quedius labradorensis				+								
	Quedius velox												
	Staphylinus pleuralis												
	Tachinus frigidus	+							+		+		

Table 3.5. Relationships between common and abundant beetle species and variables in forest structure in burned forest at the 15 year-old study site. '+' and '-' refers to positive and negative relationship respectively. Forest structure abbreviations: FC = Forest Canopy, CS = Coniferous Shrubs, SH = Shrubs, SP = Plants with Single Stems, FP = Forest-floor Plants, PM = Plants that form Mats, MO = Mosses, LI = Lichens, SN = Snags, LO = Logs, SC = Shrub-cover

Taxa	Species	FC	CS	SH	SP	FP	PM	GR	MO	LI	SN	LO	SC
Carabidae	*Calathus advena*												
	Calathus ingratus												
	Carabus taedatus												
	Elaphrus lapponicus												
	Nebria crassicornis												
	Patrobus foveocollis												
	Pterostichus empetricola												
	Pterostichus haematopus												
	Pterostichus riparius							+					
	Scaphinotus marginatus											-	
	Trechus tenuiscapus												
Staphylinidae	*Acidota quadrata*	+											
	Eucnecosum brunnescens							-					+
	Ischnosoma splendidus												
	Lordithon fungicola								+			+	
	Micropeplus laticollis												
	Mycetoporus americanus												
	Olophrum rotundicolle							-					+
	Quedius brunnipennis												
	Quedius densiventris												
	Quedius frigidus												
	Quedius labradorensis				+								
	Quedius velox												
	Staphylinus pleuralis	-		-				-					
	Tachinus frigidus												

Table 3.6. Relationships between common and abundant beetle species and variables in forest structure in burned forest at the 36 year-old study site. '+' and '-' refers to positive and negative relationship respectively. Forest structure abbreviations: FC = Forest Canopy, CS = Coniferous Shrubs, SH = Shrubs, SP = Plants with Single Stems, FP = Forest-floor Plants, PM = Plants that form Mats, MO = Mosses, LI = Lichens, SN = Snags, LO = Logs, SC = Shrub-cover

Taxa	Species	FC	CS	SH	SP	FP	PM	GR	MO	LI	SN	LO	SC
Carabidae	*Calathus advena*							-					
	Calathus ingratus												
	Carabus taedatus	+			-				-			-	+
	Elaphrus lapponicus						-						
	Nebria crassicornis								-				
	Patrobus foveocollis						-						
	Pterostichus empetricola												
	Pterostichus haematopus	+					+						
	Pterostichus riparius						-						
	Scaphinotus marginatus				+								
	Trechus tenuiscapus				+								
Staphylinidae	*Acidota quadrata*												
	Eucnecosum brunnescens												
	Ischnosoma splendidus			+									
	Lordithon fungicola												
	Micropeplus laticollis												
	Mycetoporus americanus					+							
	Olophrum rotundicolle				+			-					
	Quedius brunnipennis				+			-					
	Quedius densiventris					+		-					
	Quedius frigidus			+	+								
	Quedius labradorensis												
	Quedius velox												
	Staphylinus pleuralis												
	Tachinus frigidus												

Table 3.7. Relationships between common and abundant beetle species and variables in forest structure in fire-skips at the 15 year-old study site. '+' and '-' refers to positive and negative relationship respectively. Forest structure abbreviations: FC = Forest Canopy, CS = Coniferous Shrubs, SH = Shrubs, SP = Plants with Single Stems, FP = Forest-floor Plants, PM = Plants that form Mats, MO = Mosses, LI = Lichens, SN = Snags, LO = Logs, SC = Shrub-cover

Taxa	Species	FC	CS	SH	SP	FP	PM	GR	MO	LI	SN	LO	SC
Carabidae	*Calathus advena*							-					
	Calathus ingratus	+									+		
	Carabus taedatus												
	Elaphrus lapponicus							+			+		
	Nebria crassicornis												-
	Patrobus foveocollis	+		+									+
	Pterostichus empetricola				-								-
	Pterostichus haematopus												
	Pterostichus riparius			+						+			
	Scaphinotus marginatus	+											
	Trechus tenuiscapus				-						-	-	
Staphylinidae	*Acidota quadrata*	+						-					
	Eucnecosum brunnescens			+									
	Ischnosoma splendidus			+									
	Lordithon fungicola												
	Micropeplus laticollis						+						-
	Mycetoporus americanus												
	Olophrum rotundicolle												
	Quedius brunnipennis												
	Quedius densiventris			-	-								
	Quedius frigidus												
	Quedius labradorensis			+									
	Quedius velox												
	Staphylinus pleuralis												
	Tachinus frigidus												

Table 3.8. Relationships between common and abundant beetle species and variables in forest structure in fire-skips at the 36 year-old study site. '+' and '-' refers to positive and negative relationship respectively. Forest structure abbreviations: FC = Forest Canopy, CS = Coniferous Shrubs, SH = Shrubs, SP = Plants with Single Stems, FP = Forest-floor Plants, PM = Plants that form Mats, MO = Mosses, LI = Lichens, SN = Snags, LO = Logs, SC = Shrub-cover

Taxa	Species	FC	CS	SH	SP	FP	PM	GR	MO	LI	SN	LO	SC
Carabidae	*Calathus advena*	-									-	+	
	Calathus ingratus			-			+						
	Carabus taedatus												
	Elaphrus lapponicus												
	Nebria crassicornis												
	Patrobus foveocollis												
	Pterostichus empetricola												
	Pterostichus haematopus											+	
	Pterostichus riparius												
	Scaphinotus marginatus						-						
	Trechus tenuiscapus												
Staphylinidae	*Acidota quadrata*						-						
	Eucnecosum brunnescens												
	Ischnosoma splendidus												
	Lordithon fungicola												
	Micropeplus laticollis												
	Mycetoporus americanus												
	Olophrum rotundicolle												
	Quedius brunnipennis												
	Quedius densiventris						-						
	Quedius frigidus												
	Quedius labradorensis			+									
	Quedius velox												
	Staphylinus pleuralis												
	Tachinus frigidus												

Table 3.9. Stepwise multiple regression models for predicting epigaeic beetle diversity (total number of species) from forest structure.

Taxa	Study Sites	Forest Types	Model	Adjusted R^2	F	P
Carabidae	15 year-old burn	Mature forest	•	•	•	•
		Burned forest	- 0.90 + 1.13 (Grasses)	0.45	10.01	0.01
		Fire-skips	1.17 + 0.75 (Canopy)	0.10	4.8	0.04
	36 year-old burn	Mature forest	- 0.09 + 0.59 (Grasses) + 2.71 (Logs)	0.67	12.39	0.003
		Burned forest	4.0 - 4.0 (Snags)	0.30	5.64	0.04
		Fire-skips	0.48 + 0.30 (Single-stemmed Plants)	0.37	14.62	< 0.001
Staphylinidae	15 year-old burn	Mature forest	2.92 - 1.04 (Logs)	0.41	6.92	0.007
		Burned forest	•	•	•	•
		Fire-skips	3.97 - 0.62 (Coniferous Shrubs)	0.80	4.05	0.05
	36 year-old burn	Mature forest	•	•	•	•
		Burned forest	•	•	•	•
		Fire-skips	•	•	•	•

* refers to no independent variable being significant

Table 3.10. Stepwise multiple regression models for predicting epigaeic beetle diversity (Shannon-Weiner Index) from forest structure.

Taxa	Study Sites	Forest Types	Model	Adjusted R^2	F	P
Carabidae	15 year-old burn	Mature forest	*	*	*	*
		Burned forest	1.11 - 0.31 (Plants that form Mats)	0.39	8.12	0.17
		Fire-skips	*	*	*	*
	36 year-old burn	Mature forest	0 + 0.87 (Logs) - 0.21 (Snags)	0.67	12.18	0.003
		Burned forest	1.03 - 1.03 (Snags)	0.26	4.77	0.05
		Fire-skips	0.16 + 0.82 (Single-stemmed Plants)	0.46	20.86	0.0002
Staphylinidae	15 year-old burn	Mature forest	1.42 - 0.30 (Logs)	0.30	8.07	0.01
		Burned forest	*	*	*	*
		Fire-skips	1.20 - 0.26 (Lichens)	0.10	5.19	0.03
	36 year-old burn	Mature forest	*	*	*	*
		Burned forest	0.91 + 0.04 (Single-stemmed Plants) - 0.23 (Forest Canopy)	0.48	6.04	0.21
		Fire-skips	1.26 - 0.54 (Snags)	0.13	4.36	0.05

* refers to no independent variable being significant

Table 3.11. Stepwise multiple regression models for predicting epigaeic beetle diversity (Berger-Parker) from forest structure.

Taxa	Study Sites	Forest Types	Model	Adjusted R^2	F	P
Carabidae	15 year-old burn	Mature forest	1.07 + 0.54 (Grasses)	0.22	5.8	0.03
		Burned forest	- 0.49 + 0.74 (Logs)	0.53	13.25	0.005
		Fire-skips	1.17 + 0.75 (Canopy)	0.10	4.8	0.04
	36 year-old burn	Mature forest	0.14 + 0.06 (Single-stemmed Plants) + 1.18 (Logs)	0.72	15.17	0.001
		Burned forest	*	*	*	*
		Fire-skips	0.32 + 0.47 (Mosses)	0.33	12.19	0.002
Staphylinidae	15 year-old burn	Mature forest	2.79 - 0.51 (Logs)	0.52	6.62	0.02
		Burned forest	*	*	*	*
		Fire-skips	1.16 + 0.24 (Plants that form Mats)	0.12	5.8	0.02
	36 year-old burn	Mature forest	2.24 + 0.55 (Canopy) - 0.25 (Lichens) - 1.15 (Logs)	0.74	11.52	0.003
		Burned forest	0.17 + 0.18 (Shrubs) + 0.09 (Single-stemmed Plants)	0.53	7.11	0.01
		Fire-skips	*	*	*	*

* refers to no independent variable being significant

Table 3.12. Stepwise multiple regression models for predicting epigaeic beetle diversity (Simpson's Index) from forest structure.

Taxa	Study Sites	Forest Types	Model	Adjusted R^2	F	P
Carabidae	15 year-old burn	Mature forest	*	*	*	*
		Burned forest	*	*	*	*
		Fire-skips	* 10.42 + 7.36 (Logs)	0.14	6.9	0.01
	35 year-old burn	Mature forest	15.98 - 1.55 (Shrubs) - 0.24 (Single-stemmed Plants) - 4.77 (Logs)	0.74	11.04	0.003
		Burned forest	* 165.43 + 15.8 (Canopy) - 16.96 (Logs) + 54.17 (Mosses)	0.73	11.1	0.003
		Fire-skips	*	*	*	*
Staphylinidae	15 year-old burn	Mature forest	*	*	*	*
		Burned forest	* 17.173 + 6.36 (Lichens) + 6.06 (Snags)	0.63	10.19	0.005
		Fire-skips	*	*	*	*
	35 year-old burn	Mature forest	* 122.5 + 28.43 (Coniferous Shrubs) - 2.74 (Single-stemmed Plants) + 39.51 (Forest-floor Plants) - 105.8 (Logs) + 39.9 (Mosses)	0.89	18.52	0.001
		Burned forest	*	*	*	*
		Fire-skips	*	*	*	*

* refers to no independent variable being significant

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Chapter 4 . Thesis Conclusions

4.1 Research Summary

In Chapter 2, I assessed whether residual patches of forests, or 'fire-skips' within burns were important biotic refugia for epigaeic beetles. Results indicate that fire-skips do act as habitat reserves for litter-dwelling beetles such as *Calathus advena, Calathus ingratus, Elaphrus lapponicus, Mycetoporus americanus, Nebria crassicornis, Olorphrum rotundicolle, Pterostichus empetricola, Pterostichus haematopus, Quedius densiventris and Tachinus frigidus.* A few beetle species such as *N. crassicornis* are brachypterous (Lindroth 1961 - 69) and may require a continuum of moisture conditions to complete their life cycle (Spence 1979), and thus fire-skips appear to be relatively stable and heterogeneous habitats that may act as faunal sources.

A total of eleven rare species were collected only in habitats in and around the skips and furthermore, a glacial relict species, *P. empetricola*, (Lindroth 1961 - 69, Ball 1969, Ball and Currie 1997) was exclusively associated with the fire-skips. In contrast, to the harvest-origin edges (Spence *et al.* 1996), natural edges around both fire-skips and the surrounding mature forest promoted recolonization by forest species, and hence, enhanced faunal regeneration of the burned forest.

Tree-coring revealed that the average age of trees in fire-skips at a site burned 36 years earlier was *c.* 180 years old, while that of the surrounding

unburned forest was *c.* 72 years. Thus, fire-skips seem to be a semi-permanent part of the pyrogenic landscape, and that have survived more than one wildfire. A positive relationship between the age of the trees and fire-skip size suggests that largest skips contained the oldest evolving habitat attributes on the landscape.

Although, in contrast to species-richness hypotheses (MacArthur and Wilson 1967), there was no significant relationship between fire-skip size and total activity and richness of beetle species, larger populations of some beetles were collected in larger fire-skips. This suggests that populations of these beetles will be vulnerable to forest harvesting activities employing relatively short rotations (*c.* 100 years) in these high-elevation forests.

Overall, fire-skips seemed to provide greater landscape connectivity and a greater range of micro-habitats and were thus, vital forest patches for maintaining both late-successional, and locally endemic beetle species on fire-origin landscapes.

In Chapter 3, I determined whether habitat heterogeneity, as reflected in measures of forest composition and structure were correlated with patterns of beetle distributions. Total beetle catches and diversity were correlated primarily with overstory diversity suggesting that canopy complexity was a more important factor influencing beetles than complexity of understory vegetation *per se*. Variables of forest structure such as cover-abundance of moss, grass, canopy, undergrowth and coarse-woody debris were also positively or negatively correlated with beetle catches and diversity suggesting

association of beetles with a suite of micro-sites existing in forests (Niemelä and Spence 1994). Most of the variables in forest structure that were correlated with beetle distributions were characteristic of particular forest types, for example, grasses in burned forests and distinct forest canopy in fire-skips. Also, the range of cover-abundance of variables of forest structure in particular forest types may also explain beetle distributions, but this has not been analyzed in the present work.

Beetle diversity was correlated with almost all the twelve structure variables. However, contrary to predictions of the 'habitat heterogeneity hypothesis' (Whittaker and Levin 1977, Hart and Horwitz 1991), most of the associations were negative and thus, greater heterogeneity is not always reflected in higher species richness. Overall, results indicate that forest heterogeneity factors were important in influencing beetle distribution patterns.

4.2 Implications for Forest Management

It has been persuasively argued that with increasing anthropogenic disturbance, especially clear-cutting activities, biodiversity existing in the forests may be at considerable risk of extinctions (Erwin 1991, Wilson 1992, Hanski and Hammond 1995, Spence *et al.* 1996). Therefore, in northern landscapes produced and maintained by wildfires (Hunter 1993, Haila *et al.* 1994), forest managers must seek to emulate natural landscape patterns within harvest regimes in an effort to preserve structural complexity (Weyerhaeuser Canada 1997 a, b). However, significant questions remain

about how this should be done and if it will work (Spence *et al.* 1999). Understanding the importance of patterns and processes in pyrogenic landscapes can contribute to our ability to accomplish this emulation. This study, for example, provides the basis for the following recommendations:

(1) At the stand level, retain different sized and shaped potential residual patches consisting of fir and spruce trees, green understory and coarse woody debris. These forest patches have the potential to provide microhabitat sites to various ecological types of species, including some that are rare and endemic. Equivalent patches of Scandinavian wet spruce forest that are now generally found in matrices of cultivated and cleared land, are rich repositories of biological diversity including vascular plants, bryophytes, fungi and lichens (Söderström 1988, Kuusinen 1996, Ohlson *et al.* 1997, Hörnberg *et al.* 1998). It is possible that acting as faunal sources, these forest patches will eventually contribute to biotic regeneration of harvested landscapes.

(2) Maintain environmental heterogeneity in terms of vegetation structure and composition. This may serve especially to preserve faunal assemblages that are closely adapted to micro-sites created by specific combinations of forest attributes.

Overall, it is apparent that maintaining underlying landscape diversity and stand structure within a range of natural variability will be crucial to conserving forest-dwelling fauna (Langor *et al.* 1993, Reice 1994, Stelfox 1995, Anglestam 1997). This is especially important because harvesting

activities, as practiced here so far, create homogenous forest stands (Zackrisson 1977, Haila *et al.* 1994, Spence *et al.* 1999), and operate in much smaller time-frames than do natural disturbances.

As recommended by a conceptual fire based 'ASIO' (that refers to Absent, Seldom, Infrequent and Often fires on landscapes), sustainable forests may be maintained by simulating composition and structure of forest landscapes by operating on the same spatial and temporal continuum as natural disturbances (Anglestam and Pettersson 1997, Angelstam 1998). On the landscape scale, retention of patches would be a good option and at small scale, to further improve the retention approach, consideration of inter-patch distances (Niemelä 1996) and potential edge-effects (Spence *et al.* 1996) within retention blocks may also serve to protect species, especially those with lower dispersal rates and that are sensitive to changes in habitat conditions.

Long-term effects of forest harvesting on faunal assemblages remain to be assessed in these high elevation forests. In lodgepole pine forests in the lower foothills, evidently forest carabid beetles do not recolonize harvested blocks even 30 years post disturbance (Niemelä *et al.* 1993, Spence *et al.* 1996). Furthermore, in Europe, where forestry has persisted for centuries, studies have shown that invertebrates such as saproxylic beetles (Speight 1989, Siitonen and Martikainen 1994) and other litter dwelling species (Halme and Niemelä 1993) are at considerable risk of extinction. Therefore, we must continue efforts to develop knowledge essential to integrating natural history, ecology and forestry.

4.3 Directions for Future Research

This study should be taken as a starting point toward further understanding of the importance of landscape patterns produced by natural disturbances. Below, I suggest several research initiatives that could be usefully undertaken.

(1) The focus of this study was on litter-dwelling beetles, but a number of invertebrates and vertebrates sensitive to disturbances may also use habitats within fire-skips, especially species dependent on specific micro-sites. Therefore, long term studies on a number of taxa and their biotic interactions will serve to elucidate the role of natural disturbances in structuring natural assemblages.

(2) To evaluate ecological processes happening at regional levels, further research needs to be done on fire-skips in other habitats such as deciduous and mixed-wood forests.

(3) As harvesting creates different landscapes than wildfire, forest patches retained within harvested areas should be studied and monitored to ensure that retention blocks will continue to act as faunal storehouses.

(4) Finally, research is required on how local biota is influenced by a sum total of environmental and biotic factors operating at several ecological scales.

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Appendix 1. Species list of carabid beetles collected in the 15 and 36 year-old burn.

			15 year-old study site					36 year-old study site					
Tribes	Species Names	Classification*	Mature	Burn	Skips**	Mature Edge	Skip Edge	Mature	Burn	Skips**	Mature Edge	Skip Edge	Totals
CARABINI	*Carabus taedatus agassi* LeConte	C	1	0	0	2	1	9	5	0	2	1	21
CYCHRINI	*Scaphinotus marginatus* F. von Waldheim	A	3	2	11	1	12	4	9	19	3	43	107
NEBRIINI	*Nebria crassicornis intermedia* Van Dyke	A	17	0	157	32	85	9	2	61	0	3	366
	Leistus ferruginosus Mannerheim	R	0	0	0	0	0	0	0	0	0	2	2
NOTIOPHILINI	*Notiophilus borealis* Harris	R	0	0	2	2	0	1	2	2	1	1	11
	Notiophilus directus Casey	R	1	0	1	0	0	1	0	0	1	1	5
	Notiophilus semistriatus Say	R	0	0	0	0	0	0	0	0	3	0	3
ELAPHRINI	*Elaphrus l. lapponicus* Gyllenhal	C	0	1	7	0	20	0	18	3	0	30	79
BROSCINI	*Miscodera arctica* Paykull	R	0	2	1	2	4	0	2	0	3	0	14
TRECHINI	*Trechus tenuiscapus* Lindroth	C	2	6	3	6	5	0	2	1	0	10	36
BEMBIDIINI	*Bembidion bimaculatum* Kirby	R	0	0	1	0	0	0	0	0	0	0	1
	Bembidion concolor Kirby	R	1	0	1	0	3	0	0	0	0	0	5
PATROBINI	*Patrobus foveocollis* Eschscholtz	C	1	1	3	1	6	0	2	1	0	6	21
PTEROSTICHINI	*Pterostichus adstrictus* Eschscholtz	R	0	0	1	2	5	0	0	0	1	0	9
	Pterostichus punctatissimus Randall	R	5	2	0	0	1	0	0	1	1	5	15
	Pterostichus haematopus Dejean	A	17	0	153	46	22	8	34	59	17	20	376
	Pterostichus empetricola Dejean	C	0	0	28	0	9	0	0	9	0	1	47
	Pterostichus riparius Dejean	A	5	26	47	70	130	0	2	15	8	29	332
AGONINI	*Calathus ingratus* Dejean	C	0	1	12	17	19	2	5	1	7	1	65
	Calathus advena LeConte	A	77	0	72	6	29	59	28	10	40	0	321
	Agonum cupreum Dejean	R	0	1	0	0	0	0	0	0	0	0	1
	Agonum quinquepunctatum Motschulsky	R	0	1	6	0	11	0	0	0	0	0	18
	Agonum placidum Say	R	0	0	1	0	1	0	0	0	0	0	2
	Platynus mannerheimii Dejean	R	3	0	0	0	0	0	0	1	0	1	5
AMARINI	*Amara hyperborea* Dejean	R	0	0	0	2	1	0	2	0	2	1	8
	Amara erratica Duftschmid	R	0	0	0	0	1	0	0	1	0	0	2
	Amara pseudobrunnea Lindroth	R	0	0	0	0	0	0	2	0	0	1	3
HARPALINI	*Harpalus nigritarsus* Sahlberg	R	0	1	0	1	1	0	0	0	0	0	3
	Harpalus solitaris Dejean	R	0	0	0	1	0	0	0	0	0	0	1
LEBIINI	*Cymindis unicolor* Kirby	R	0	0	2	0	0	0	0	0	0	0	2
CLIVININI	*Dyschirius timidus* Lindroth	R	0	0	0	0	0	3	0	0	0	1	4
Total number of individuals			133	44	509	191	366	96	115	184	89	157	1884
Total number of species			12	11	19	14	20	9	14	14	13	18	31

* R - Rare species
C - Common species
A - Abundant species
** Includes the 0m trap at the skip-edge

Appendix 2. Species list of staphylinid beetles collected in the 15 and 36 year-old burn.

			15 year-old study site					36 year-old study site					
Tribes	Species Names	Classification*	Mature	Burn	Skips**	Mature Edge	Skip Edge	Mature	Burn	Skips**	Mature Edge	Skip Edge	Totals
PROTEININAE	*Proteinus* species	R	1	0	4	1	4	0	0	0	0	0	10
EUSPHALERINI	*Eusphalerum* species	C	1	1	2	0	36	0	0	0	2	0	41
ANTHOPHAGINI	*Acidota quadrata* Zetterstedt	C	7	2	16	13	0	0	0	7	1	9	55
	Olophrum rotundicolle Sahlberg	C	7	1	4	0	0	0	5	22	1	40	80
	Eucnecosum brunnescens Sahlberg	C	4	1	14	13	3	0	4	10	1	23	73
	Phlaeopterus cavicollis Fauvel	R	0	0	1	0	1	0	0	0	0	0	2
	Anthobium reflexicolle Casey	R	0	0	4	0	0	0	0	0	0	0	4
TACHYPORINI	*Tachinus frigidus* Erichson	C	16	0	16	9	11	9	2	8	4	3	78
	Tachinus tachyporides Horn	R	0	0	0	0	0	0	0	2	0	5	7
	Tachinus quebecensis Robert	R	7	0	1	0	7	1	2	0	1	0	19
	Tachyporus nimbicola Campbell	R	0	1	0	4	7	0	0	0	1	1	14
BOLITOBIINI	*Lordithon fungicola* Campbell	C	5	17	5	12	12	6	11	9	13	3	93
	Mycetoporus smetanai Smetana	R	0	0	1	0	0	0	0	0	0	2	3
	Mycetoporus americanus Erichson	C	1	0	1	1	2	9	9	2	0	12	37
	Mycetoporus nigrans Smetana	R	1	1	1	3	8	0	0	1	2	0	17
	Ischnosoma splendidus Gravenhorst	C	2	8	4	5	11	0	3	1	1	11	46
	Ischnosoma pictum Horn	R	0	2	2	1	1	0	0	0	0	0	6
	Bryoporus smetanai Smetana	R	0	0	0	0	0	0	1	2	0	0	3
	Bolitobius species	R	0	0	0	1	0	0	0	0	0	0	1
OLIGOTINI	*Stenus* species	R	0	2	0	0	0	1	0	5	0	5	13
PHILONTHINI	*Philonthus concinnus* Gravenhorst	R	0	1	0	0	0	0	0	0	1	0	2
	Philonthus furvus Nordmann	R	0	1	0	0	0	0	0	0	0	0	1
STAPHYLININI	*Staphylinus pleuralis* LeConte	C	9	3	0	26	2	0	0	0	0	0	40
QUEDIINI	*Quedius frigidus* Smetana	C	0	1	0	2	3	0	10	19	3	64	102
	Quedius velox Smetana	C	0	2	2	3	8	6	0	13	1	4	39
	Quedius labrodroensis Smetana	A	6	19	66	45	273	21	28	32	33	152	675
	Quedius transparens Motschulsky	R	0	0	1	0	0	0	0	0	0	0	1
	Quedius brunnipennis Mannerheim	A	19	3	43	6	2	27	5	25	3	55	188
	Quedius densiventris Casey	A	30	1	136	3	16	28	13	6	10	0	243
	Quedius fulvicollis Stephans	R	0	3	6	3	13	0	1	0	0	0	26
OTHIINI	*Atrecus macrocephalus* Nordmann	R	0	0	1	0	0	0	0	0	0	3	4
MICROPEPLINI	*Micropeplus laticollis* Mäklin	C	1	0	2	1	0	2	0	8	1	7	22
Total number of individuals			117	70	333	152	419	110	94	172	79	399	1945
Total number of species			16	19	23	19	19	10	13	17	17	17	32

* R - Rare species
C - Common species
A - Abundant species

** Includes the 0m trap at the skip-edge

Appendix 3. Formulae used for calculating diversity and dominance measures (adopted from Magurran 1988).

1. Shannon-Weiner Diversity Index-

$H' = \Sigma\, p_i \log p_i$

Where p_i, the proportional abundance of the *i* th species = (n_i / N).

2. Berger-Parker Diversity Index-

$d' = N_{max} / N$

Where N= total number of individuals and N_{max} = number of individuals in the most abundant species.

3. Simpson's Index-

$S' = \Sigma\, \{[(n_i (n_i - 1)]/ [N (N - 1)]\}$

Where n_i = number of individuals in the *i* th species, and N = the total number of individuals.

Appendix 4. Vegetation classification at the two study sites. 0 = absent, 1 =≤ 1%, 2 = 1.1-20%, 3 = >20% cover

Species	15 year-old burn			36 year-old burn		
	Mature	Burn	Skips	Mature	Burn	Skips
Forest Canopy						
Abies lasiocarpa (Hook.) Nutt.	1	0	2	1	1	2
Picea engelmannii Parry ex Engelm.	0	0	1	0	0	1
Picea mariana Mill.	0	0	1	0	0	2
Pinus contorta Loudon	2	1	1	2	1	0
Coniferous Understory						
Abies lasiocarpa (Hook.) Nutt.	1	0	1	1	1	1
Pinus contorta Loudon	0	2	1	1	1	0
Shrubs/ Multi-stemmed Plants						
Betula glandulosa Michx.	1	2	1	1	2	1
Fragaria virginia Duchesne	0	0	0	1	1	1
Ledum glandulosum Nutt.	2	2	1	3	2	1
Lupinus arcticus [L.]	1	1	1	0	0	0
Prunus virginia L.	1	0	0	0	1	0
Rhododendron albiflorum Hook.	1	0	0	0	0	0
Ribes glandulosum Grauer	0	0	1	0	0	0
Ribes lacustre (Pers.) Poir.	1	1	1	0	0	0
Rubus species	2	1	2	1	0	1
Salix species	1	1	1	2	2	2
Vaccinium membranaceum Dougl. Hook. ex	2	1	1	2	2	1
Viburnum edule Michx.	0	0	0	0	0	1
Single-stemmed Plants						
Arnica cordifolia Hook.	1	1	1	1	1	1
Arnica latifolia Bong.	1	1	1	1	1	1
Aster species	1	1	1	0	0	0
Castilleja miniata Douglas. ex. Hook.	0	1	0	0	0	0
Disporum trachycarpum (S. Wats.) B. & H.	0	0	1	0	1	1
Epilobium angustifolium L.	1	2	1	1	2	1
Epilobium ciliatum Raf.	0	0	1	0	0	0
Equisetum species	2	2	2	1	2	2
Leguminosae	0	0	0	1	0	1
Mertensia paniculata (Ait.) G. Don.	1	1	1	0	0	0
Parnasia fimbriata Konig	0	0	1	0	0	0
Pedicularis species	0	0	1	1	1	1
Petasites palmatus Ait.	1	1	1	1	1	2
Potentilla rivalis Nutt.	0	0	0	2	1	1
Solidago species	1	1	1	1	2	1
Taraxacum officinale Weber	0	1	0	0	0	0
Umbelliferae	0	0	0	0	0	1
Forest-floor Plants						
Caltha leptosepala DC.	0	0	0	1	1	1
Linnaea borealis L.	1	1	1	2	1	1
Mitella nuda L.	0	0	0	1	1	1
Moneses uniflora L.	0	0	1	0	0	1
Pyrola species	0	0	0	0	0	1
Cornus canadensis L.	2	2	2	2	2	2
Plants that form mats						
Empetrum nigrum L.	2	1	1	1	1	1
Saxifraga tricuspidata Rottb.	0	0	1	0	0	0
Vaccinium vitis-idaea L.	2	1	1	2	2	2
Lycopodium species	1	0	1	2	2	1
Grasses	1	2	1	1	2	2
Mosses	3	3	3	3	3	3
Lichens	1	1	1	2	2	1
Snags	1	2	1	1	1	1
Logs	2	2	2	1	1	1
Shrub Cover	2	2	2	2	2	2